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Assessing Growth Response to Climate Controls in a Great Basin Artemisia Tridentata Plant Community

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ASSESSING GROWTH RESPONSE TO CLIMATE CONTROLS IN A GREAT BASIN *ARTEMISIA TRIDENTATA* PLANT COMMUNITY

by

Lorenzo Apodaca

Bachelor of Science in Biochemistry
University of Nevada, Las Vegas
2009

A thesis submitted in partial fulfillment
of the requirements for the

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ABSTRACT

Assessing Growth Response to Climate Controls in a Great Basin *Artemisia Tridentata* Plant Community

by

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An assessment of the growth response of key vegetative species to climatic variability is vital to identifying possible local impacts on ecosystems faced with imminent climate change. With current climate projections in Nevada predicting a shift to an even more arid climate with greater year-to-year variability, the imperative exists to identify the effects of specific climatic controls on plant growth and to research methods to assess large-scale vegetative changes, especially in more remote areas where readily available data sets may be lacking. This study utilized annual growth ring indices constructed from big sagebrush (*Artemisia tridentata* ssp. *tridentata*) stems collected in Spring Valley, NV as a measure of vegetative growth and compared standardized measures of ring growth to records collected from climate monitoring stations within the region. Growth ring indices had a strong, positive correlation with total hydrologic-year precipitation (Oct-Sep; $r = 0.82$, $p < 0.001$) with precipitation totals measured at the nearest climate station for the months of January, March, April, and June being the most highly related to ring growth ($r = 0.48, 0.36, 0.47$, and 0.41, respectively; $p < 0.05$). Mean maximum growing season temperatures were found to be negatively correlated to growth during the months of April, May, June, and October of the previous year ($r = -0.40, -0.37, -0.50$, and -0.30, respectively; $p < 0.001$). Multiple regression analyses between ring width measurements and relevant climate controls suggest that projected climate changes will be largely detrimental to the overall growth of big sagebrush in Spring Valley. Historical NDVI (Normalized Difference Vegetation Index), an indicator of plant canopy leaf area and photosynthetic activity, was regressed against sagebrush ring indices to examine growth response through time. NDVI values in May performed reasonably well as an indicator of sagebrush ring growth when measurements were integrated over all available sagebrush sites ($r^2 = 0.48$, $p < 0.01$), but this relationship was inconsistent when assessed on a site-by-site basis when comparing single-pixel NDVI measurements against site-specific sagebrush growth ring chronologies. Overall, sagebrush growth ring chronologies were found to perform very well as a climate proxy and comparisons between sagebrush ring widths and a network of ring records from other species revealed that sagebrush growth in Spring Valley is representative of the larger region.

ACKNOWLEDGEMENTS

This project put me through a gamut of emotion ranging from jubilant optimism to unnerving frustration, but the good news is that the myriad of individuals I met along the way helped to keep me mostly contained on the more positive side of that spectrum. First and foremost, I would like to thank my advisor, Dr. Dale Devitt. His zeal for knowledge was the best motivator one could ask for, and thankfully his patience is as limitless as the many great ideas he carries around in his skull at any given time. If nothing else, it's that same intellectual curiosity that I hope to keep buttoned to my lapel for the rest of my days (that and how to dig a hole and fill it back up – a Devitt lab specialty!). I would also like to acknowledge the many contributions provided by my academic committee members, Dr. Stanley Smith and Dr. Paul Schulte, but I would especially like to thank Dr. Lynn Fenstermaker. Lynn rightfully earns the title of Busiest Person I Have Ever Known, and despite her countless duties and academic pursuits, she never failed to find the time to lend me her expertise or send me "positive eye energy" (which I'm now convinced is an actual thing). All of these people ultimately helped shape this document into what it is.

I joined the Devitt lab many years ago as an undergraduate at UNLV, and since the place inexplicably exerts its own gravitational force on its former students, I had no choice but to return for my graduate studies. Luckily, it's populated by people I enjoy being around so I didn't mind. Lena Wright, Brian Bird, and Amanda Wagner all volunteered their assistance over the course of this project, begrudgingly or otherwise, and helped keep the atmosphere full of laughs even during those times where we were all

too exhausted to walk. There were many other people whom I didn’t encounter on such a day-to-day basis but would still like to acknowledge: Fred Landau for assisting me greatly with sample collection, Dene Charlet for managing the many aspects of my assistantship, Mallory Eckstut for being my EPSCoR travel buddy, Scott Strachan from UNR for providing me with useful dendrochronology advice, the Ely Bureau of Land Management office for granting me the proper permits, and the Nevada EPSCoR administrators and staff for not only extending me this great opportunity but also providing a great environment in which to do research.

And finally, I would like to thank the support and stability of my home life. It is not a debt I could ever itemize (not that I would want to!) nor is it one I could ever truly settle, but I imagine I will have to try soon enough.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The regional productivity and distribution of arid-land vegetation in the desert Southwest will likely be impacted by changes in climatic controls relevant to plant growth. Ecological responses attributed to human-induced climate change have already been documented (Walther *et al*. 2002), and future shifts in current temperature and precipitation regimes will likely affect susceptible species for decades to come. Nevada is expected to experience an average increase in temperature of approximately 1.6-2.1 ºC in the spring and fall and by 2.7-3.3 ºC in the winter and summer by 2100 (HadCM2 model, EPA 1998). Projected changes for precipitation are less conclusive, but measurable increases and decreases of between 5 and 10% have been recorded in parts of Nevada and nearby states (USGCRP 2009). Climate change in the desert Southwest is projected to be characterized by increased aridity and climatic variability (Seager *et al*. 2007). Further defining the relationship between climate and plant growth could allow for a clearer understanding of future vegetative responses to continued climate change.

The annual growth rings characteristic of many woody shrubs have proven to be a useful tool in the retrospective analysis of climate-plant relationships (Rayback and Henry 2005, Bar *et al*. 2007, Forbes 2010). Growth ring studies such as these operate off of the basic assumption in dendroclimatology that states that ring-producing plants living near the boundaries of their ecological ranges exhibit ring width patterns that reflect the climatic controls most limiting to growth (Fritts 1976). Therefore, annual growth rings measured from suitable plants have been used to assess the climate variables most significant to local vegetative productivity. However, the majority of research efforts concentrate on the ring growth of conifers and deciduous trees, and vegetation zones, such as those dominated by shrubs, are underrepresented in the literature.

Sagebrush species dominate the Great Basin shrub steppe, which covers a large portion of the state of Nevada. The shrub is found across approximately 500,000 square kilometers over 14 U.S. states and 3 Canadian provinces (Connelly 2004). Within Nevada, big sagebrush inhabits many of the numerous high elevation valleys that dominate the state's landscape. Few studies have attempted the analysis of sagebrush growth rings using traditional dendrochronological techniques despite it possessing a distinct annual growth ring pattern (Diettert 1938, Biondi *et al*. 2007). Multiple studies have been conducted that highlight the value of sagebrush species in their respective habitat. Removal of sagebrush has been linked to changes in soil nutrient distribution (Inouye 2006, Bechtold and Inouye 2007), and its disappearance is thought to promote invasion by cheatgrass (*Bromus tectorum*) (Knapp 1996, Chambers *et al*. 2007), which in turn can lead to more frequent and intense wildfire events (d'Antonio and Vitousek 1992, Brooks and Pyke 2001) and further shifts in community dynamics (Young and Evans 1978, Wisdom *et al*. 2002). Sagebrush stands are also highly associated with a multitude of other species, with some of these being sagebrush-obligates that rely entirely on sagebrush for their continued survival (Best 1972, Swenson *et al*. 1987, O'Farrell 1974, Hobbs *et al*. 1996, Connelly *et al*. 2004).

Purpose of Study

This study examines the growth response of the woody shrub *Artemisia tridentata* (big sagebrush) in Spring Valley, Nevada (Figure 1.1) to climatic variability. Current sagebrush productivity and distribution could potentially be impacted by projected temperature increases and shifts in precipitation regimes associated with global climate change. Further definition of the relationship between climate and sagebrush growth and providing a method for which to assess growth over multiple scales would allow for a clearer understanding of climate change impacts on future sagebrush distribution.

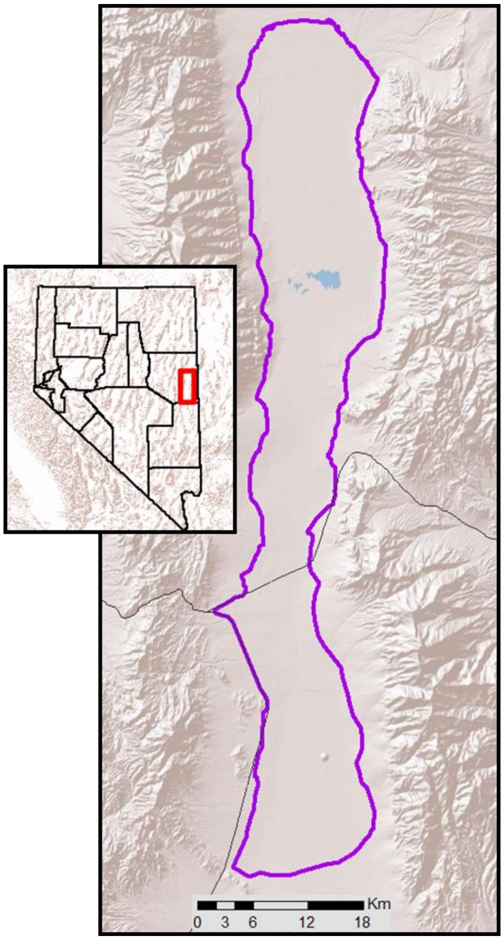


Figure 1.1 Approximate area of Spring Valley.

To examine the role of interannual climate variability on big sagebrush growth, annual growth ring width indices, a standardized measure of year-to-year plant productivity, were constructed using stems collected from plant stands within Spring Valley. The growth ring indices were compared to historical climate records collected from climate monitoring stations located in and around the valley. Bootstrapped correlation analysis was used to determine which climate variables were most closely correlated with sagebrush ring growth and to identify what time periods these correlations were most significant. Growth environments can vary greatly across ecological gradients present in Nevada, so sagebrush growth ring indices were also compared to ring indices from studies conducted in surrounding mountain ranges to assess potential spatial variability in growth response to climate across the immediate region and to lend evidence to the use of sagebrush as a comparable climate proxy. Regression analysis was also used to establish an empirical relationship between ring growth and satellite-derived vegetation indices to provide a method to assess sagebrush growth over multiple scales.

Hypotheses

The following hypotheses were tested:

1) Annual growth rings of big sagebrush growing in Spring Valley will show a high degree of commonality in their year-to-year growth that can be attributable to climate.

2) The interannual pattern of big sagebrush annual ring growth will differ from ring growth in surrounding forests.

3) Climate controls on big sagebrush in Spring Valley will be mainly dominated by total winter (October-February) precipitation as winter snowpack has been documented as a major source of growing season moisture, and this correlation between ring growth and winter precipitation will be strongly positive.

4) Earlywood and latewood ring widths in Spring Valley big sagebrush are influenced by late-winter/early growing season precipitation and late growing season precipitation, respectively.

5) Growing season NDVI measurements averaged across all sites and assessed at the individual pixel level will show a significant positive relationship with valley-wide and site-specific sagebrush ring chronologies, respectively.

CHAPTER 2

BACKGROUND

Big Sagebrush in Nevada

Plant life is intrinsically linked to climate because climate plays a substantial role in species distribution, phenology, and year-to-year growth, and because of this intimate link, global climate change phenomena have the potential to greatly influence existing and future vegetation. Big sagebrush (*Artemisia tridentata*) is the dominant component of the sagebrush steppe ecosystem that covers at least 45% of the Great Basin land area (West 1983). Pollen records have lent evidence that sagebrush species have persisted in western North America for more than 30,000 years (Van Devender and King 1977), and likely due to its extensive history and pervasive presence in the region, the existence of this shrub is tightly linked to many facets of the Southwest. Being such an integral part of the landscape in the state, Nevada adopted sagebrush as its state flower in 1917, decorated its flag with sagebrush sprays, and it retains the unofficial nickname of the "Sagebrush State." However, with increased human development of the West, starting as far back as the first Euro-American settlers, sagebrush distribution has become more and more fragmented (Welch 2005), and the looming effects of climate change could impact these plant communities even further.

Basin big sagebrush (ssp. *tridentata*) is one of several subspecies of sagebrush that inhabit the western U.S. It occupies the lowest elevational range of all the sagebrush species (600 to 2100 m), typically growing in the deeper, more fertile soils of mountain valleys (USDA, NRCS 2013). It is also the largest and longest-lived of all the subspecies, growing as high as four meters with plants reportedly ranging from 30-210 years of age (Ferguson and Humphrey 1959). As a desert species, it displays many adaptations for dealing with its semi-arid environment. The small, tridentate leaves are covered with dense trichomes, which contribute to reduced water losses and the signature silvery color of the plant (Diettert 1938). The root structure of sagebrush is very extensive, with the major portion of the root network situated within the upper soil zones allowing for the utilization of ephemeral summer storms (Sturges 1977, Donovan and Ehleringer 1994). Deeper roots are able to extract moisture from the lowest soil zones and were shown by Richards and Caldwell (1987) to function in hydraulic lift where soil water from these deeper layers is nocturnally transported upwards by the plant and redistributed to shallower soils for use during the much more water-demanding daylight hours.

Perhaps the most interesting morphological feature of the sagebrush plant is the stem. In his definitive publication on sagebrush anatomy, Diettert (1938) first described the “marked eccentricity” of the sagebrush stems that is characterized by the sometimes complex lobed shape of the stem’s circumference. He attributed these eccentricities to the death of the plant’s reproductive structures and localized cambium death resulting from the removal of the bark, both of which resulted in deep depressions in the wood structure. Distinct stem lobes were formed by future wood growth expanding around these voids in the stem. In sufficiently aged plants, these lobes have a tendency to separate from the oldest portion of the stem, and from each other, forming “rosette” structures, according to Ferguson (1964).

The wood of sagebrush, as described by Diettert (1938), is structured as diffuse porous with vessels mainly populating the early season wood (earlywood), lending it a lighter color, and dense structural fibers making up the darker and more substantial late season wood growth (latewood). The interxylary cork layer, however, was the most striking feature of the stem, according to Diettert, and gives the shrub a clearly recognizable growth ring pattern. This cork layer exists between the very last cells of a given ring and the very first cells of the next season's growth. Cork growth actually occurs during the earlier part of the growing season, and its development is attributed to a small layer of meristematic cells that remain in the inner portion of the stem. The annual ring patterns of big sagebrush, accentuated by this distinctive interxylary cork layer, can be exploited due to their close relationship with dry climates, as will be discussed in the next section.

Understanding the Climate and Sagebrush Growth Relationship Using Dendrochronology

The concept of climatic influence on the widths of tree rings was conceived by many historical figures over recent centuries, including the great Leonardo da Vinci (Stallings 1937), but the modern study of dendrochronology stems from work done at the turn of the 20th century by A.E. Douglass (Speer 2010). Since then, the scientific study of tree rings has evolved significantly, incorporating more sophisticated techniques, and has been applied to a wide variety of wood-producing plants, including big sagebrush.

To help understand the underlying theory in studies such as this one, there are a few concepts in dendrochronology defined by Fritts (1976) and Speer (2010) that merit a brief discussion here: (1) the principles of limiting factors, (2) the aggregate tree model, and (3) standardization. The principle of limiting factors states that growth in an organism is controlled by the most limiting environmental factor (Speer 2010). For example, a sapling growing underneath a densely populated forest canopy would be limited by access to sunlight, if all other factors remain favorable. Once the plant is able to break through the canopy, sunlight is less limiting, and growth may become controlled by another factor, such as soil moisture. In ring-producing plants, it is presumably this most limiting factor that controls ring width and makes it possible to use ring widths as proxies for climate, assuming that the limiting factor is readily identifiable. In arid and semi-arid environments, many plant communities will be most limited by water availability (Fritts 1976).

While trees may be most limited by only one or a few factors, the principle of the aggregate tree model proposes that tree growth does in fact record everything that affects growth. The model, as presented by Cook (1985), is:

$$R_t = f(G_t, C_t, D1_t, D2_t, E_t)$$

where R_t is ring width at year *t*, G_t is the age-related growth trend, C_t is the climate factor, $D1_t$ and $D2_t$ are endogenous and exogenous stand disturbances, respectively, and E_t is an error term incorporating all other possible factors. The age-related growth trend describes the tendency for tree rings to narrow as the plant gets older and results from both the naturally slower growth of older trees and the geometric issue of adding equal amounts of wood onto a cylinder of ever-increasing width. The possible complexity in ring growth that is suggested by this model highlights the importance of proper site selection as one would prefer to choose plants that are largely controlled by the factor or factors of interest with minimal contribution to growth from extraneous factors. For example, if climate is the signal of interest, which it often is in these studies, then site selection should focus on sites that are relatively free of any stand disturbances.

Lastly, the principle of ring standardization describes techniques used to amplify the signal of interest present in tree ring measurements while reducing unwanted noise. The general method of standardization is to take a time series of correctly dated raw ring width measurements and mathematically transform that data into ring width indices using a pre-determined growth curve model that estimates expected growth throughout the length of the series. The types of growth models and the mathematical functions used to create ring index values are numerous, and their application is typically based on *a priori* knowledge of the organism and study area. A useful approach to tree ring standardization was first described by Cook and Peters (1981) – the smoothing spline. The spline approach was lauded for its ability to remove unwanted variance in the tree ring series due to the highly flexible nature of the spline parameters. The downside to the approach was the possibility of removing a large portion of the desired variance related to the growth signal of interest due to the potential for spline curves to over-fit ring series.

The first ring studies to incorporate these techniques on big sagebrush were conducted by Ferguson and Humphrey (1959) and Ferguson (1964). This research spanned a large portion of western North America, and both studies were able to draw some general conclusions on the link between sagebrush ring growth and climate, most notably a link with precipitation. In his analyses, Ferguson noted a common tendency for sagebrush to produce “false rings”, or ring patterns that appear as two or more discrete rings within one year’s growth and warned that this behavior was more prevalent towards the species’ southernmost extent.

The frequency in which false rings were present was a concern for its use in dendrochronological study so Biondi *et al*. (2007) published a study confirming the annual nature of sagebrush rings. They were able to use radiocarbon dating to trace the location of the 1963-64 ^{14}C “bomb spike” that was attributed to Cold War-era, aboveground nuclear testing to correctly date rings in a small sampling of sagebrush stems taken near Ely, Nevada. No false or absent rings were identified in their stems. Although this lent strong evidence to the annual nature of the rings, their small number of useable stems didn’t allow for the construction of a viable ring chronology.

Aside from Ferguson (1959), a few studies have examined the associations between climate and growth in sagebrush species. Cawker (1980) counted rings to determine age structure and recruitment patterns in sagebrush stands growing in southern British Columbia, and recruitment indices created from these data was regressed against climate data. Multiple regression models using seasonal and monthly climate variables were able to account for up to 50% of the variance present in stand age structure. Recruitment was determined to be dependent on a variety of climate factors, including summer dryness, early spring temperatures, heavy fall rain, and extreme low winter temperatures. These results were indicative of a complex relationship between sagebrush and climate stemming from the high degree of variability in the growth conditions inherent in sagebrush habitat.

Perfors *et al*. (2003) used an interesting approach to examine growth response in the wood of mountain big sagebrush (ssp. *vaseyana*) to experimentally-induced warming. The entire stem structure of their sagebrush stems was meticulously dismantled at each branching point and twig cohorts of similar age were grouped together. Ring areas from these cohorts were used to calculate wood volume in a given year, and these measurements were used to construct growth curves to estimate an intrinsic growth rate.

Differences in growth rates were examined over several experimental plots where heaters were employed to assess the effect on sagebrush. They found a significant positive link between growth rates and early snowmelt date induced by artificial warming, lending evidence to the potential impacts of global climate warming on the growth and distribution of mountain big sagebrush. However, their methods were unrealistic for larger sample sizes, and their technique did not lend itself to building a viable ring chronology.

Poore *et al*. (2009) employed ring width measurements of mountain big sagebrush in Colorado to examine their relationship with annual, monthly, and seasonal climatic factors. Their small sample size (n=5) prevented the use of ring chronology building techniques, and their standardization procedure did not include any detrending that likely weakened their results by introducing noise in the ring widths unattributed to climate. Despite these possible hindrances, they were able to conclude that a significant negative correlation between shrub growth and warmer summer temperatures could lead to decreased productivity in existing sagebrush stands if predicted temperature increases were to occur in the future.

The Biological Significance of NDVI

Remote sensing, specifically the Normalized Difference Vegetation Index, has a history of use in Spring Valley and surrounding valleys. With plans for large-scale groundwater extraction coming to fruition within the last decade, there existed a need for accurate assessments of water resources within Spring Valley, and Landsat-based NDVI proved to be a useful tool for valley-wide estimations of plant activity, notably evapotranspiration (ET). By establishing an empirical relationship between single-pixel NDVI measurements and ET estimated over a pixel area, Devitt *et al*. (2010) were able to account for up to 79% of the variation in ET at selected Spring Valley study sites, with significant relationships also found in other nearby valleys (r^2 values between 0.61 and 0.81). They found that single-pixel values of NDVI provided equal or greater regression coefficients compared to values integrated over 5 x 5 pixel squares, thereby demonstrating the ability of NDVI to capture plant processes at very fine scales. In a related study (Baghzouz *et al*. 2010), ground-based NDVI measurements were taken over a growing season (May-October) using individual radiometer sensors mounted over various shrubs, including big sagebrush, in a Spring Valley mixed-shrub community. Significant relationships were found between these measurements and several sagebrush plant parameters, including tissue nitrogen concentration, leaf xylem water potential, and leaf area index, thereby lending greater biological significance to NDVI values. A comparison was made between these ground-based measurements and satellite-based NDVI, also derived from Landsat imagery, taken over the same locations, and large differences were observed between the two. Ground-based NDVI values were noticeably higher than satellite values, more so in the vegetation-sparse Spring Valley site, and the progression of plant phenology through the growing season was more readily apparent in ground-based NDVI data compared to satellite-based measurements. These differences in the ability of the two methods to capture plant phenology were attributed to the larger synoptic view of the satellite that integrated reflectance patterns from all surface components, particularly soil, which dominated the overall reflectance signal.

The issue of cross effects was noted in a study by Lopatin *et al*. (2006) as a possible limitation of satellite measurements' ability to capture variation in tree ring growth in the Komi Republic, Russia. In this study, PAL-NDVI measurements with an 8 km cell size were correlated with standardized ring width chronologies of spruce and pine species growing within the boreal forest region. Their values were statistically significant, but they theorized that the large grid size could have been unrepresentative of the local growing conditions from which their trees were sampled from.

Wang *et al*. (2004) were able to demonstrate a very strong relationship (r = 0.91) between tree ring growth in oak trees (*Quercus* ssp.) in a Kansas grassland and NDVI extracted from National Oceanic and Atmospheric Administration Advanced Very High Resolution Radiometer (NOAA/AVHRR) satellite imagery. Window sizes centered around their sampling sites ranged from 7 x7 pixels (59 km^2) to 11 x 11 pixels (146 km^2), and their strongest results came from comparisons using their smallest window size. Although no rationale was given for the disparity in results, it is not unreasonable to assume that the smaller window size was more representative of the growth conditions experienced by their sampled trees.

CHAPTER 3

MATERIAL AND METHODS

Site Selection and Sample Collection

Big sagebrush (*Artemisia tridentata* ssp. *tridentata*) stem cross-sections were collected during nine trips between February and July of 2011 in Spring Valley, NV. Sampling sites were chosen based on the presence of suitably sized plants (Figure 3.1). Care was taken to avoid sites where plants might have possible access to shallow groundwater, sites containing signs of heavy disturbance, or sites that could potentially receive enhanced precipitation runoff. Three to five sagebrush stems were collected at each sampling site with each plant being located within an arbitrary 30x30 m^2 plot, corresponding to the area of an individual Landsat image pixel. A minimum distance of 3 km between sites was maintained. Within Spring Valley, big sagebrush is mainly dominant in the southern portion of the valley, with stands being much sparser in the middle area and completely absent in the northern region where soils become more saline and phreatophytes dominate.

Canopy dimensions and leaf area index were measured prior to stem harvesting. LAI measurements were taken using a Decagon AccuPAR-LP80 meter (Decagon Devices, Inc., Pullman, WA, USA). Individual sagebrush stem cross-sections were collected by sawing the main stem at or slightly above ground level. Above-ground biomass of each plant was then measured with a hanging scale. A subsample of the main stem was trimmed off of the cut end, labeled, and placed in a paper bag for transport back to the lab. Soil samples were collected from each site at 20-cm increments up to a maximum depth of one meter using a manual soil auger to assess soil texture, moisture and salinity. Each 20-cm increment was bagged and analyzed separately. One set of soil samples was collected per site, but a sampling depth of one meter was not achievable at all sites. GPS coordinates of each site were also recorded to the nearest 3 m to relate each sagebrush site location with its respective pixel in a satellite image scene.

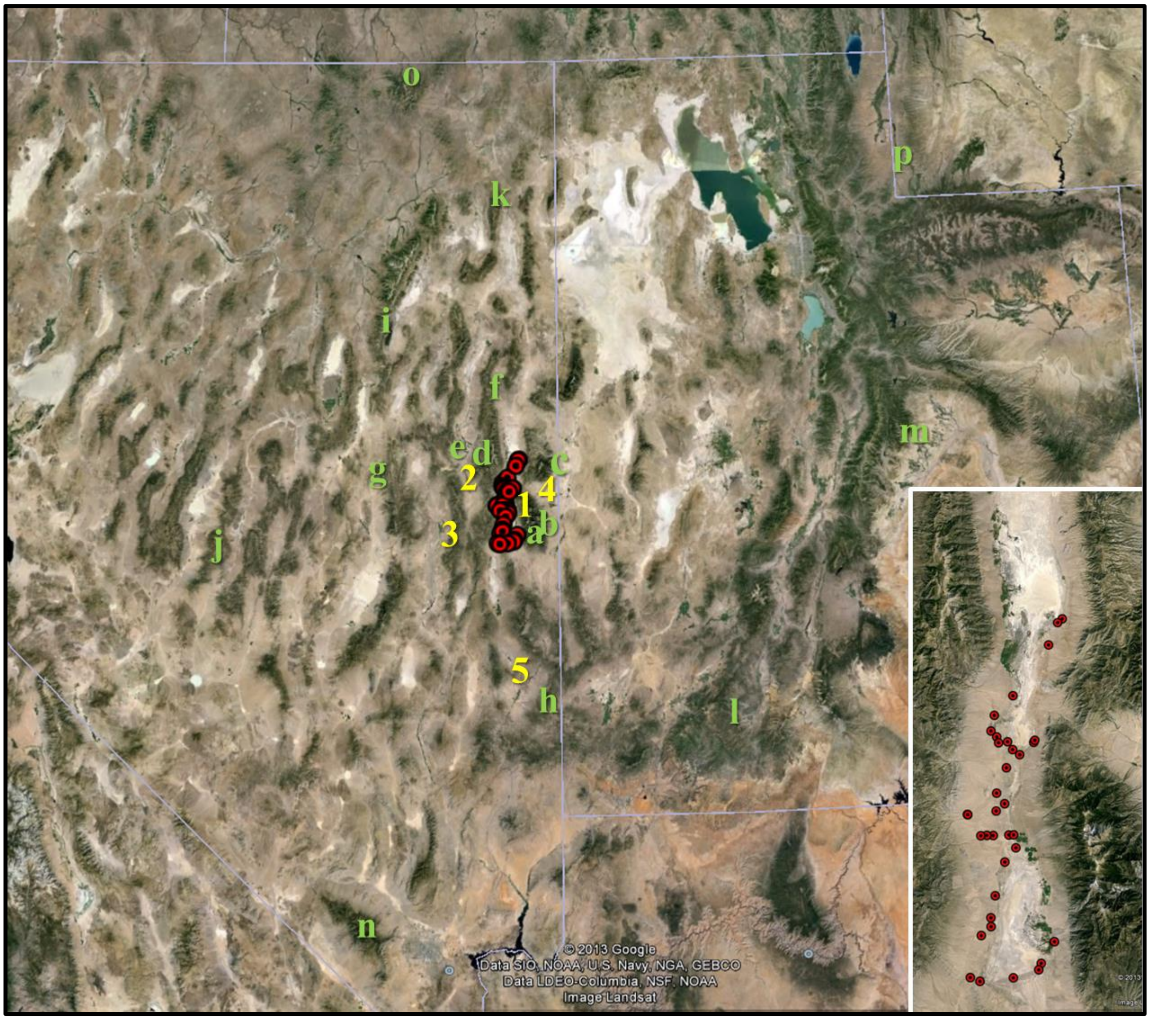


Figure 3.1 Spring Valley site map. Yellow numbers show the approximate location of the climate monitoring stations (1, Shoshone; 2, Ely; 3, Lund; 4, Great Basin National Park; 5, Pioche). Green letters show the approximate locations of ring chronologies used for comparisons with sagebrush (location names listed in Table 4.4) Red markers indicate sagebrush sampling sites. The inset is a zoomed view of the sampling sites.

Stem Processing and Ring Width Measurement

A subsample cross-section was trimmed off of the larger collected stem and prepped for measurement by sanding with increasingly finer grit sandpaper until the individual rings were clearly visible (Figure 3.2). Sagebrush stems possess a characteristic lobed appearance that develops as a result of localized cambial death. Because of the lobed nature of the stems and harsh desert conditions, some of the cross-sections were highly fragmented and were unsuitable for further use. The remaining samples had at least one lobe available for ring measurements. Many stem cross-sections were missing the innermost portion of the stem including the pith, but had an adequate portion of the stem available for ring measurements.

Figure 3.2 Spring Valley sagebrush shrub (left) and stem (right). The cut stem shows its ring pattern and lobate structure. The hole in the sample is likely the work of a wood-boring insect.

Ring measurements were taken to the nearest micrometer using a Velmex tree-ring measuring stage (Velmex, Inc., Bloomfield, NY, USA) positioned under a digital stereo microscope and connected to a laptop monitor to assist with viewing.

Measurements were recorded on another laptop using MeasureJ2X tree-ring measuring software (http://www.voortech.com/projectj2x/). Individual ring measurements were taken along an arbitrary radius drawn through the middle of each existing lobe starting with the outermost ring and ending at the innermost ring (or pith, when present). Up to four radii were measured for each stem depending on the number of distinct lobes present on the stem. Measurements were taken starting with the outermost ring, because the exact year associated with this ring was known, either 2010 or 2011, depending on when the stem was harvested.

Each individual ring measurement consisted of two separate measurements, an earlywood and latewood width. Total ring width was calculated by the measurement software as a sum of these two widths. Earlywood and latewood were differentiated from each other due to the highly contrasting colors of the two wood types. Whenever a clear early/latewood pattern was not present, a single ring width measurement was taken. The boundaries of individual growth rings in big sagebrush are easily identified by an inter-xylary layer of cork cells. Growth ring width was defined as the shortest linear distance between the innermost (closest to the pith) boundary of cork cells from the previous ring and the innermost boundary of the measured ring's cork layer. This allowed the cork layer to be included in the total width measurement.

Ring Series Standardization

Ring width series standardization is necessary for removing low-frequency trends present in the data that could be considered noise and to remove differences in growth rates between samples (Fritts 1976). For this study, a smoothing cubic spline was fit to each measured ring series (one per radius) and width measurements were standardized by taking the ratio of the measured widths to the fitted values. To create site-specific ring width chronologies, ring indices of radii measured from a single site were averaged using a robust mean. Ring indices from all measured radii were averaged using a robust mean to construct a stand-level, total ring width chronology that incorporated the common year-to-year growth signals of all Spring Valley sagebrush.

All steps of the detrending and ring chronology construction process, including associated descriptive statistics, were performed following the dendrochronological methods outlined by Cook and Kairuikstis (1990) and by using the statistical program R (R Development Core Team, 2009) and the Dendrochronology Program Library in R (dplR) package (Bunn 2008). Data quality control and generation of ring chronology statistics were done using dplR and the tree ring cross-dating program COFECHA (Holmes 1983).

Climate Data Acquisition

All historical precipitation and temperature data were downloaded from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC) land-based station data archives (http://www.ncdc.noaa.gov/data-access/land-based-station-data). Data from climate monitoring stations in or near Ely, Lund, Pioche, and the Great Basin National Park were collected (Figure 1). Data from these stations spanned between 1938 and 2010. Climate data from a station located within Spring Valley near the Shoshone Ranch was also collected, and this record spans between 1989 and 2007. Precipitation data was downloaded as a monthly total from all stations.

Daily precipitation totals were downloaded from the Shoshone station only. Temperature data were also downloaded, including mean monthly, mean monthly minimum, mean monthly maximum and monthly extreme minimum/maximum, from all stations.

Remote Sensing and NDVI

NDVI values corresponding to each sagebrush sampling site were extracted from Landsat 5 TM scenes acquired during the growing season months (March-September) of 1986-2010. All images were downloaded from the USGS Earth Resources Observation and Science Center (EROS) via the Global Visualization (GLOVIS) tool (http://glovis.usgs.gov/) and processed using the image processing software, ENvironment for Visualizing Images (ENVI) (Exelis Visual Information Solutions, Boulder, CO, USA). As many cloud-free scenes were collected for each year as possible with a maximum of two scenes per month, but due to the satellite's 16-day orbit and the randomness of cloud cover, some months were represented by only one image or are missing images entirely. The images acquired during the years of 1995 and 1998 were especially problematic as they were exceptionally wet years with extensive cloud cover through much of the growing season.

To estimate NDVI, reflectance values were extracted from scenes collected from bands 3 and 4 (red and near-infrared bands, respectively) of the Landsat 5 TM satellite. After radiometric calibration was performed using the ENVI Landsat calibration algorithm (based on Chandler *et al*. 2009), field spectra, corresponding to light, medium, and dark targets, were used to atmospherically correct and normalize reflectance data using the empirical line method (Farrand *et al*. 1994, Smith and Milton 1999). Field spectra acquired with a FieldSpec Pro (Analytical Spectral Devices, Inc., Boulder, CO, USA) with 1 nm spectral resolution were converted to Landsat TM bandwidths using the ENVI Spectral Library Resampling tool, which employs a Gaussian model based on the TM band wavelength and full-width at half maximum (FWHM) sensitivity of the Landsat TM detector for the conversion. The resulting converted field reflectance spectra and corresponding average Landsat TM pixel radiances were used to develop regression equations for the empirical line atmospheric correction. Downloaded images were previously terrain corrected and georectified by EROS. NDVI was calculated for each sagebrush sampling site from each available Landsat image using the following equation (Rouse *et al*. 1974):

$$NDVI = \frac{R_{NIR} - R_{RED}}{R_{NIR} + R_{RED}}$$

where R_{NIR} was the reflectance value from the near-infrared band 4 (0.76-0.90 µm) of the satellite's multi-spectral scanner and R_{RED} was the reflectance value from the red band 3 (0.63-0.69 µm). Values were averaged into site-specific annual and monthly measurements as well as across all 36 sites to produce an annual and monthly measure of Spring Valley sagebrush NDVI at two different scales.

Percent vegetative cover was assessed from aerial photographs provided by the Southern Nevada Water Authority using unsupervised pixel classification within the ENVI software environment to map green cover.

Statistical Methods

All ordinary least squares analyses and multiple regressions were performed using SigmaStat 11.0 (SPSS, Inc., Chicago, IL, USA). Backward stepwise regression was also used to determine the best combinations of climatic variables and plant/site parameters that could account for the greatest amount of variation present in sagebrush ring widths. Regression results were considered acceptable if individual predictor variables had a variance inflation factor (VIF) of less than 2, and the sum of all VIFs was less than 10. The degree to which variables of interest were correlated with sagebrush ring widths are reported using Pearson's r statistic, and predictive regression relationships between NDVI and sagebrush rings are summarized with coefficients of determination (r^2).

Bootstrapped correlation coefficients between the sagebrush chronology and climate variables were calculated using DendroClim2002 software (Biondi and Waikul 2004). Coefficients were assessed by correlation of the total width sagebrush chronology against each monthly climate variable. The significance and stability of the coefficients were tested with 1000 bootstrap estimates by random extraction of data points with replacement from the original data set. To use the shorter Shoshone data sets effectively with this program, it was necessary to extrapolate values beyond the available record length. This was done using linear regression between the Shoshone data sets and other available data sets of more suitable length from nearby climate stations. Shoshone had the closest linear relationship with Lund ($r^2 = 0.90$) and Ely ($r^2 = 0.92$) for annual precipitation and temperature, respectively, and each was used to extrapolate monthly measurements for use in DendroClim2002.

A few statistics and statistical methods were used in this study that are unique to dendrochronological study. The mean series intercorrelation coefficient (r) is a statistic that describes the mean correlation of individual ring series to the larger stand-level chronology and represents the common stand-level signal recorded for a site (Speer 2010). The viable portion of the ring chronology was determined using the Estimated Population Signal (EPS) defined in Speer (2010):

$$EPS = \frac{t * r}{t * r + (1 - r)}$$

where r is the mean series intercorrelation coefficient and t is the average number of tree series accounted for in the chronology. A threshold value of 0.85 was used, and the portion of the final chronologies that fell below this threshold was not used in determining climate relationships. Mean sensitivity (MS) describes the year-to-year variability in ring measurements (Douglass 1936). Its value ranges from 0 to 1, where a mean sensitivity value approaching 1 indicates a ring series that is highly sensitive to some environmental factor. High MS values can be problematic as they are associated with consistently false or missing annual rings and associated rings can be difficult to accurately date (Speer 2010). Finally, the first-order autocorrelation (ar1) estimates the degree to which the previous year's growth affects growth in the subsequent year.

CHAPTER 4

RESULTS

Plant and Site Characteristics

A total of 36 individual sagebrush sampling sites, representing the sagebrush population in Spring Valley, were selected for the study. Sites were located in the elevation range of 1681-1856 m. Plant composition at each site ranged from homogenous sagebrush (22 sites) to mixed shrub (14 sites) communities where sagebrush had a co-dominant presence along with greasewood (*Sarcobatus vermiculatus*). Percent vegetative cover measured across all sites had a mean value of 26.9 ± 7.5%. Textural analysis of surface soils (0-20 cm) collected at 32 of the 36 sites identified the soil texture as sandy loam at 21 sites, loam at 8 sites, loamy sand at 2 sites, and clay loam at 1 site. Soil salinity measurements identified eight sites with saline soil profiles (mean $EC_e \geq 4$ dS/m, 0-100 cm sampled at 20 cm increments).

Stem cross sections were collected from 118 individual sagebrush plants in Spring Valley. Plants varied greatly in height (118.5 ± 26.8 cm), canopy volume (7.1 ± 6.1 m^3), aboveground biomass (4.3 ± 2.8 kg), and stem cross sectional area (30.4 ± 21.1 cm^2). Plant canopy LAI had a mean value of 0.88 ± 0.36, however measurement conditions were not standardized and almost one-fourth of plants were not measured for LAI due to cloudy conditions. Individual ring width measurements across all stem cross sections exhibited a mean ring width of 1.03 ± 0.29 mm and a mean ring count of 39.5 ± 13.1 rings per stem. Correlative relationships between site and plant variables are summarized by the correlation matrix shown in Table 4.1.

The main climatic variables used in regression analyses with sagebrush ring chronologies are summarized in Table 4.2. Precipitation in and around Spring Valley was highly variable during the recorded intervals (Figure 4.1, top left). The Shoshone monitoring station, the only station within the valley itself, received an average of 24.3 cm of precipitation each year with most of that precipitation falling during the growing season months (March-September). Precipitation measured at Shoshone most closely resembled measurements taken at the Ely (23.4 cm) and Lund (25.3 cm) stations. Rainfall measured at the Pioche and Great Basin National Park (GBNP) sites was higher on average (34.2 cm and 33.5 cm, respectively), but its seasonal distribution followed the same relative pattern as the rest of the region. Monthly precipitation measured over the 1989-2007 interval at Shoshone Ranch (Figure 4.1, bottom left) showed no clear trends in precipitation throughout the year other than slightly dryer conditions towards the end of the calendar year (November-December).

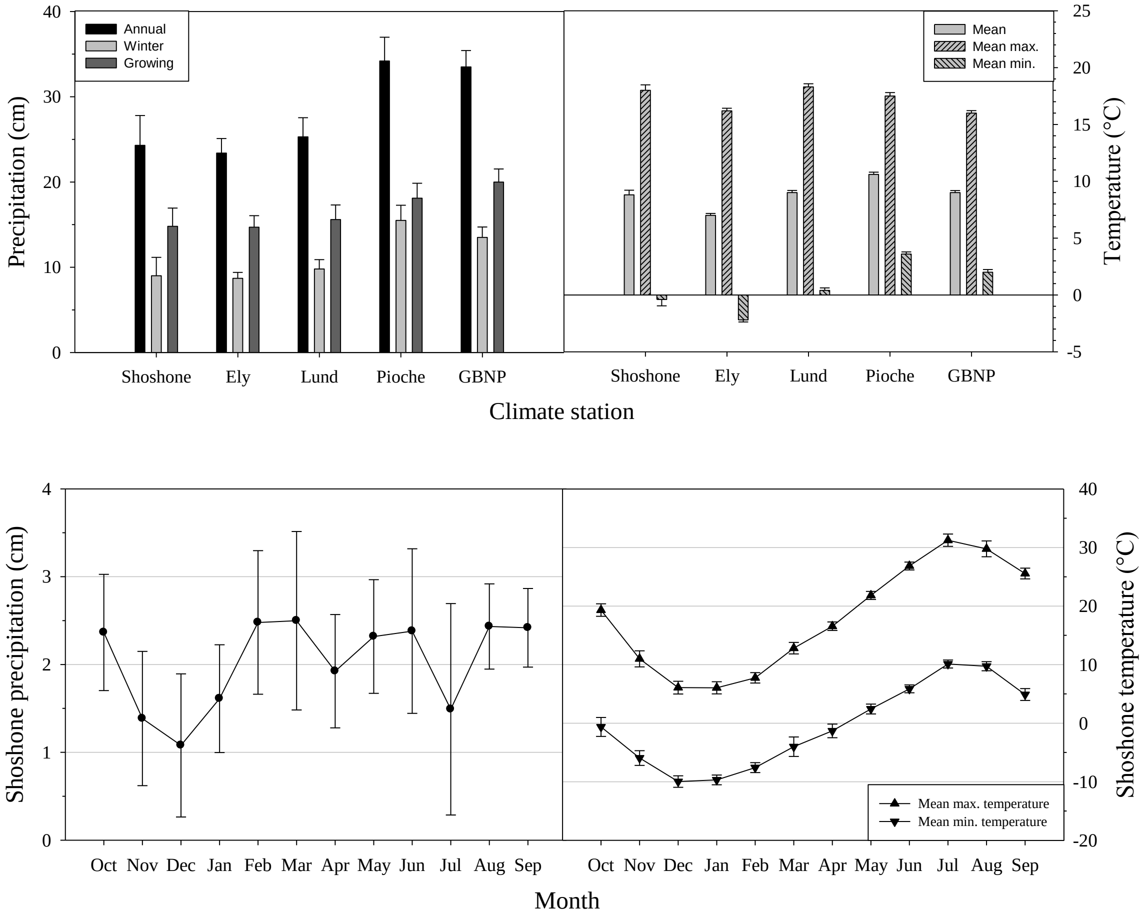


Figure 4.1 (Top) Summaries of measurements collected from each climate station. Average precipitation totals (left) and temperature averages (right). GBNP, Great Basin National Park station. Annual = hydrologic growth year (Oct-Sep), Winter = Oct-Feb, Growing = Mar-Sep. (Bottom) Mean monthly precipitation and temperature for the Shoshone station (1989-2007). All error bars denote the 95% confidence interval.

Temperature measurements were much less variable compared to rainfall and varied little throughout the area (Figure 4.1, top right). Shoshone Ranch temperatures averaged 8.8 °C annually with an average daily temperature range between -0.4 and 18.0 °C. Monthly minimum and maximum temperature averages showed a sinusoidal pattern with the hottest temperatures occurring in July and the coolest temperatures occurring in December and January.

Sagebrush Chronologies

An average sagebrush growth ring width chronology spanning the time period of 1942-2010 was constructed from 247 measured radii of 103 stem cross sections (Figure 4.2) and incorporated 9753 individual ring measurements. All sampling sites were represented in the stand-level index except for SV11, which was not included in the chronologies, as all plants from this site exhibited erratic ring patterns that could not be satisfactorily dated. The sagebrush ring chronology showed a high degree of inter-series agreeability as demonstrated by a relatively large inter-series correlation coefficient of 0.613 (Table 4.3). Significant correlations were obtained when comparing the sagebrush chronology with the surrounding network of tree ring width chronologies reported from other studies (Table 4.4). These other study sites spanned a range of elevations (1852-3415 m) and distances as far away as 350 km. A significant relationship ($p < 0.05$) was found in 13 of the 16 chronologies. Elevation or distance from Spring Valley showed no clear influence on the strength of the correlation and subsequently on the relatedness of each chronology with the sagebrush chronology.

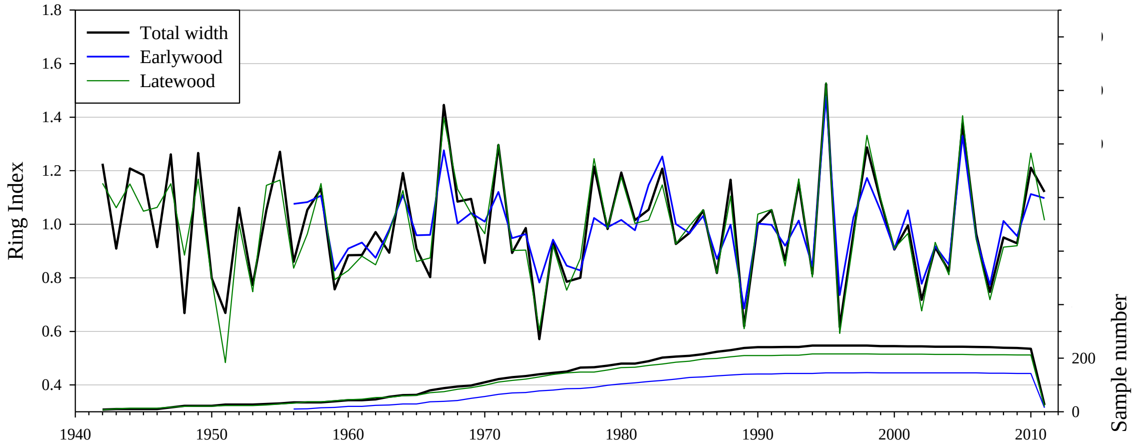


Figure 4.2 Spring Valley sagebrush ring chronologies constructed using total ring width (black), earlywood width (blue), and latewood width (green). Number of available samples is shown on the right axis.

Earlywood and latewood ring width chronologies were also constructed from all available stem cross sections. The early/latewood growth pattern was inconsistently present in the collected stems, so the number of radii represented by each ring index varied from the other indices, as did their respective EPS intervals (Table 4.3). Earlywood and latewood ring widths showed small root mean square errors when compared to the total ring width chronology, 0.09 mm and 0.05 mm, respectively, implying little difference in growth response between the measurement types, so all further analyses were done using total ring width measurements only. Individual, site-specific ring width indices varied greatly in their respective year ranges and inter-series correlations (Table 4.5).

Sagebrush Rings and Climate

The sagebrush chronology exhibited a significant, positive correlation with all annual and seasonal precipitation totals from all five meteorological monitoring locations

(Figure 4.3) using ordinary correlation analysis. Precipitation from the Shoshone Ranch monitoring station, the only one present within Spring Valley itself, produced the highest correlation between annual growth year precipitation and ring widths (r = 0.82, p < 0.001), however data for this station was only available for the years 1989-2007. Annual growth year precipitation totals measured at the remaining four stations - Ely, Lund, Pioche, and GBNP - showed comparatively weaker, but still highly significant correlations with ring widths (r = 0.67, 0.65, 0.69, 0.53, respectively; all p < 0.001). Winter and growing season precipitation totals measured at all climate stations sites showed significant correlations with ring widths, but these regressions showed a weaker relationship than those using annual precipitation totals (r-values between 0.35 and 0.68).

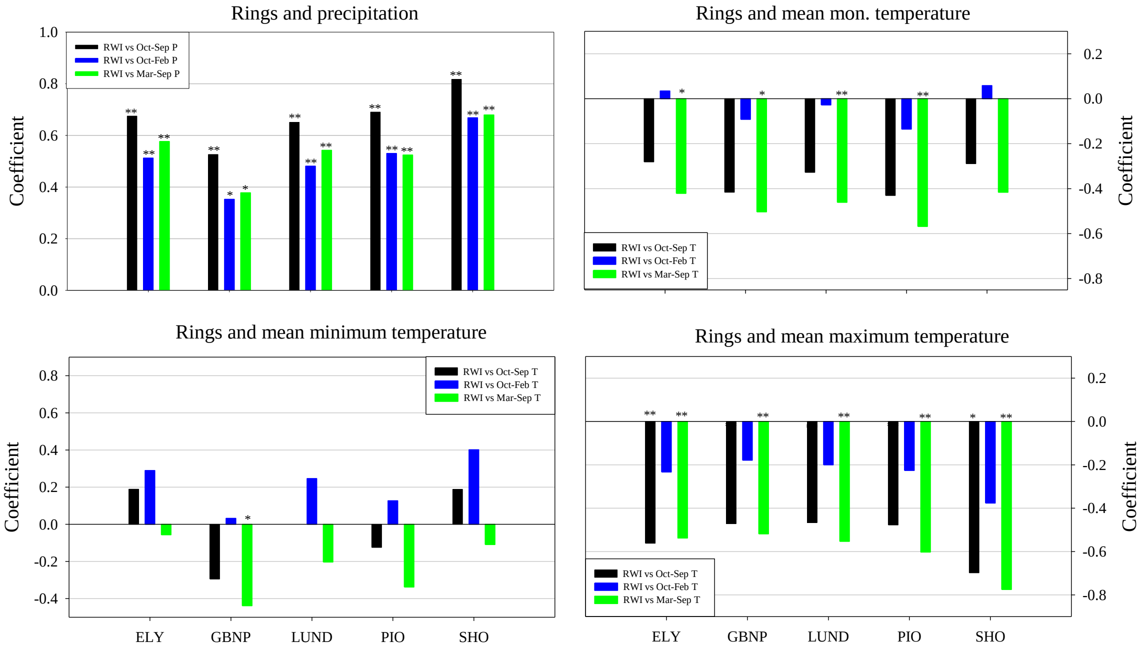


Figure 4.3 *Artemisia tridentata* ring chronology correlations with annual and seasonal climate. Meteorological measurements were taken at Ely, Great Basin National Park (GBNP), Lund, Pioche (PIO), and Shoshone Ranch (SHO). (*p < 0.01, **p < 0.001)

Mean maximum growing season temperatures measured at all stations demonstrated a significant and negative effect on sagebrush ring index values (Figure 4.3) using ordinary correlation analysis, and again, measurements from the Shoshone station produced the best relationship ($r = -0.78$, $p < 0.001$). No significant relationships between ring growth and mean maximum or mean minimum cool-season temperatures were discovered with the exception of one significant correlation between ring width and mean minimum growing season temperature measured at the GBNP station ($r = 0.44$, $p < 0.001$).

Bootstrapped correlation analysis between sagebrush ring widths and extrapolated Shoshone monthly precipitation (Figure 4.4) demonstrated positive and significant ($p < 0.05$) correlations for the months of January ($r = 0.48$), March ($r = 0.36$), April ($r = 0.47$), and June ($r = 0.41$). Ely monthly precipitation showed a similar series of significant positive relationships during the month of January and from March through June (coefficients between 0.29 and 0.56, Figure 4.5). Lund monthly precipitation showed a monthly pattern identical to Shoshone Ranch (correlations between 0.23 and 0.49) with the exception of an additional significant correlation between ring growth and precipitation occurring in November of the previous year ($r = 0.23$). Monthly precipitation recorded at the nearby GBNP showed significant positive correlations with ring growth in January ($r = 0.28$), April ($r = 0.50$), and May ($r = 0.23$). Monthly precipitation in Pioche had significant correlations with ring growth in February ($r = 0.30$), March ($r = 0.27$), and April ($r = 0.30$), but had some monthly correlations not present in the other data sets in August ($r = -0.25$), September ($r = 0.27$), and October of the previous year ($r = 0.28$).

Mean monthly and mean monthly maximum temperatures showed many significant negative relationships with sagebrush growth in Spring Valley, with most of the impact occurring during the late spring and early summer months (Figures 4.4-4.6). Bootstrapped correlations between ring widths and Shoshone Ranch, Lund, and Ely maximum temperatures were similar in magnitude and showed an identical pattern of significance ($p < 0.05$, Figures 4.5-4.6) with negative relationships occurring during the months of April (Shoshone Ranch, $r = -0.40$; Lund, $r = 0.40$; Ely, $r = -0.42$), May (Shoshone Ranch, $r = -0.37$; Lund, $r = 0.45$; Ely, $r = -0.34$), June (Shoshone Ranch, $r = -0.50$; Lund, $r = 0.54$; Ely, $r = -0.48$), and the October of the previous growing season (Shoshone Ranch, $r = -0.30$; Lund, $r = -0.28$; Ely, $r = -0.33$). Maximum temperature recorded near GBNP and Pioche had significant negative associations with ring growth during the months of April ($r = -0.40$ and $r = -0.34$, respectively) and June ($r = -0.37$ and $r = -0.46$, respectively). Associations between ring growth and mean minimum monthly temperatures were less consistent throughout the five sites. Shoshone Ranch minimum temperatures showed no significant relationships with ring growth throughout the 15-month period. June minimum temperatures measured at Ely had a significant negative relationship with ring growth ($r = -0.24$). Lund minimum temperatures measured in January ($r = 0.36$), May ($r = -0.27$), and June ($r = -0.40$) were also related to ring growth. GBNP and Pioche minimum temperatures had significant negative correlations with ring growth during April ($r = -0.31$ and $r = -0.26$, respectively) and June ($r = -0.35$ and $r = -0.30$, respectively). At GBNP, August minimum temperatures were also positively correlated with ring growth ($r = 0.35$). Correlations with mean monthly temperatures largely reflected those of mean maximum temperature (Figures 4.4-4.6). However, those correlations were weaker and are likely indicative of the stronger effect of temperature minimums and maximums on plant growth.

Relationships identified from bootstrap analysis largely agreed with those obtained from ordinary correlation analysis (Figure 4.4). Among the Shoshone Ranch and Ely data sets, the only point of consistent disagreement between the two methods was for January mean monthly and minimum monthly temperatures. Ordinary correlation analysis yielded large, significant, and positive correlations for the Shoshone Ranch data, and correlation values that were consistently outside the range of the expected bootstrapped coefficients for Ely data. Such a large discrepancy with the Shoshone Ranch data could be explained by the fact that the abbreviated, 18-year data set was used for ordinary correlation analysis, resulting in relationships that might have been reduced in strength had those particular climate records been as lengthy as the four others. However, with a similar, but lesser, discrepancy present between the Ely coefficients, such an association between January temperature and ring growth is possible and makes physiological sense as temperature during the early snowmelt period could have sizable effects on water availability and early shoot growth.

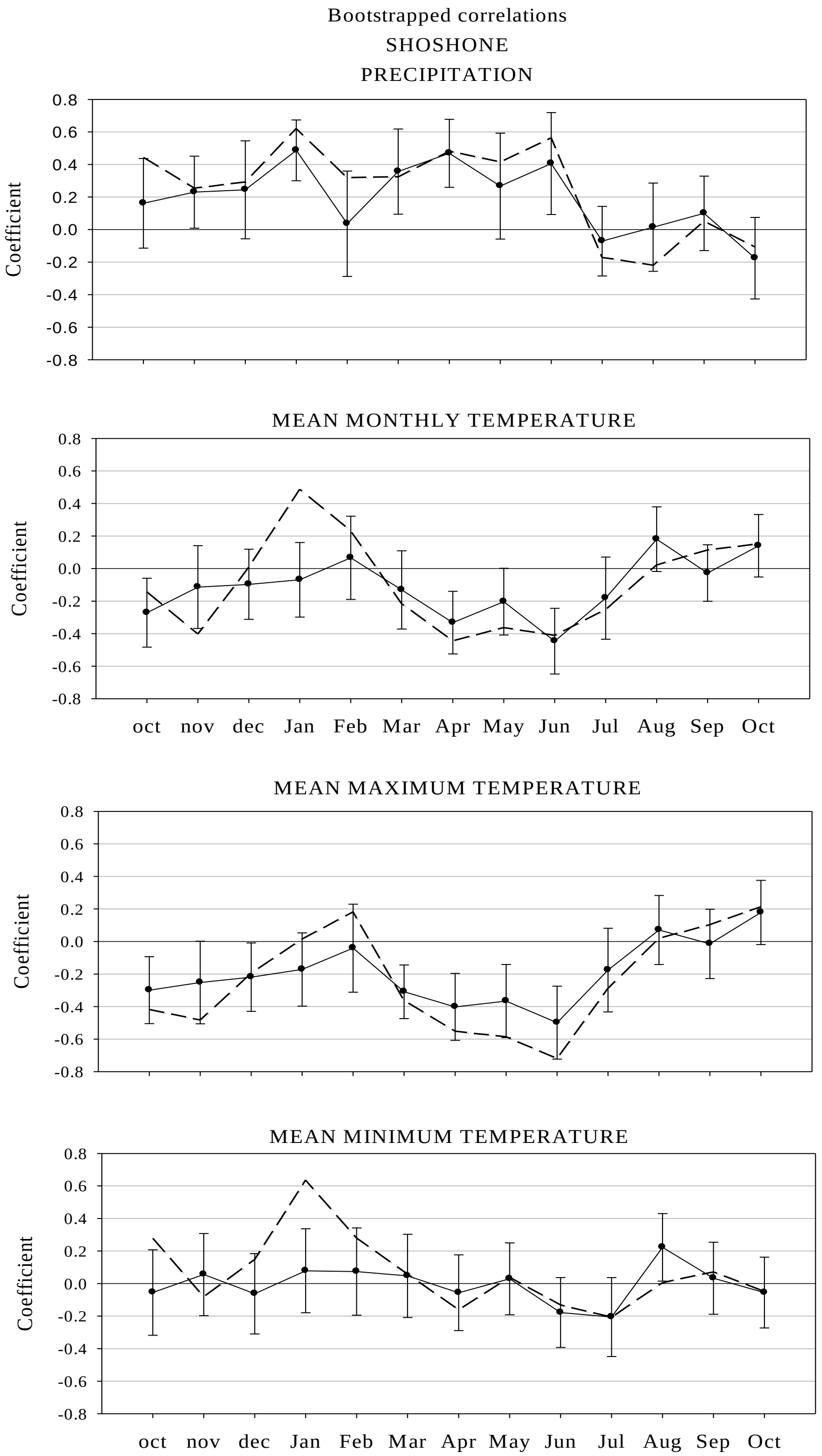


Figure 4.4 Bootstrapped monthly correlation results – Shoshone Ranch. Coefficients are shown with their 95% confidence interval ranges. The dashed line shows coefficient results from non-bootstrapped correlation analysis using the Shoshone Ranch 1989-2007 data set. Months from the previous year are not capitalized.

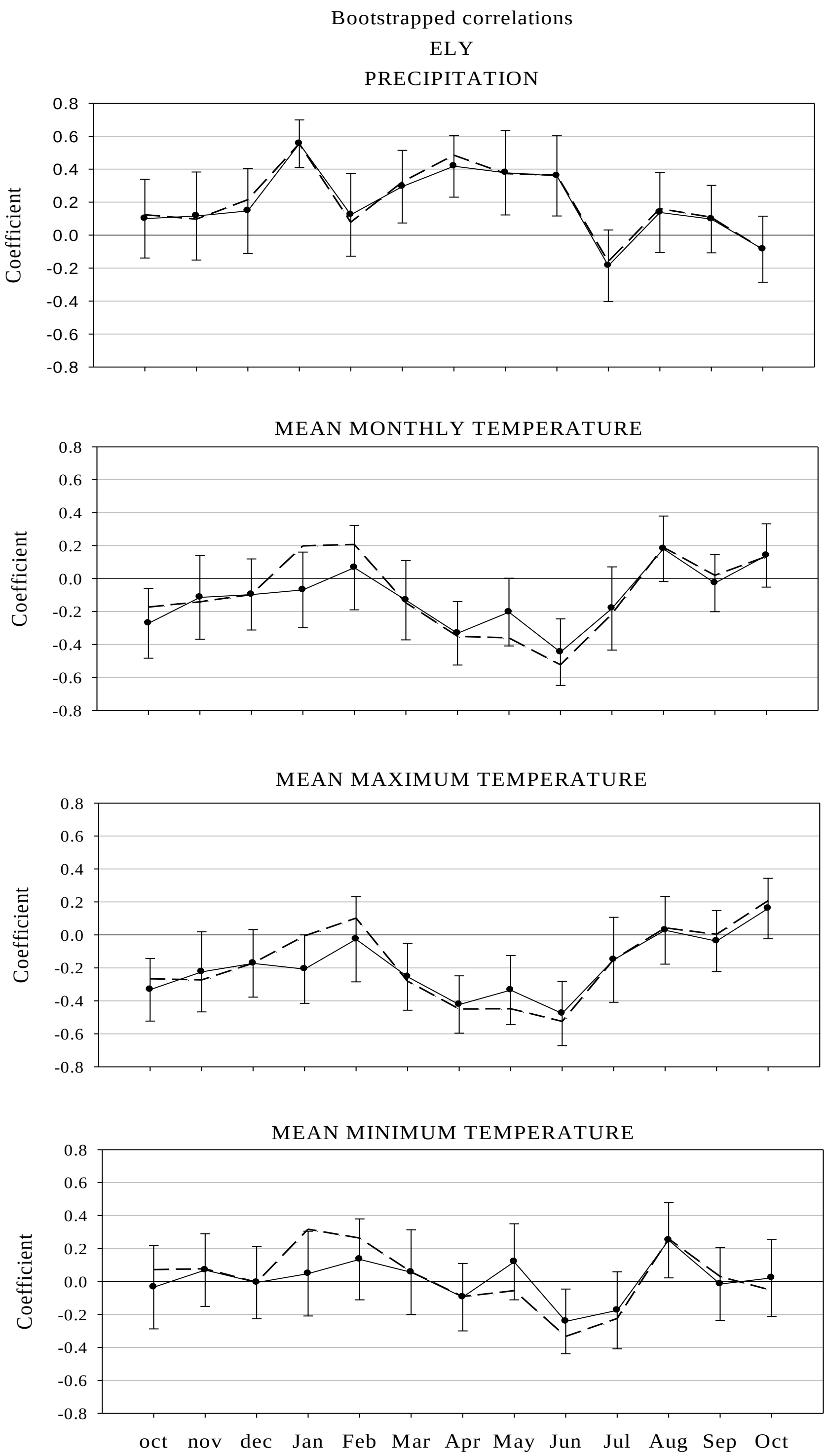
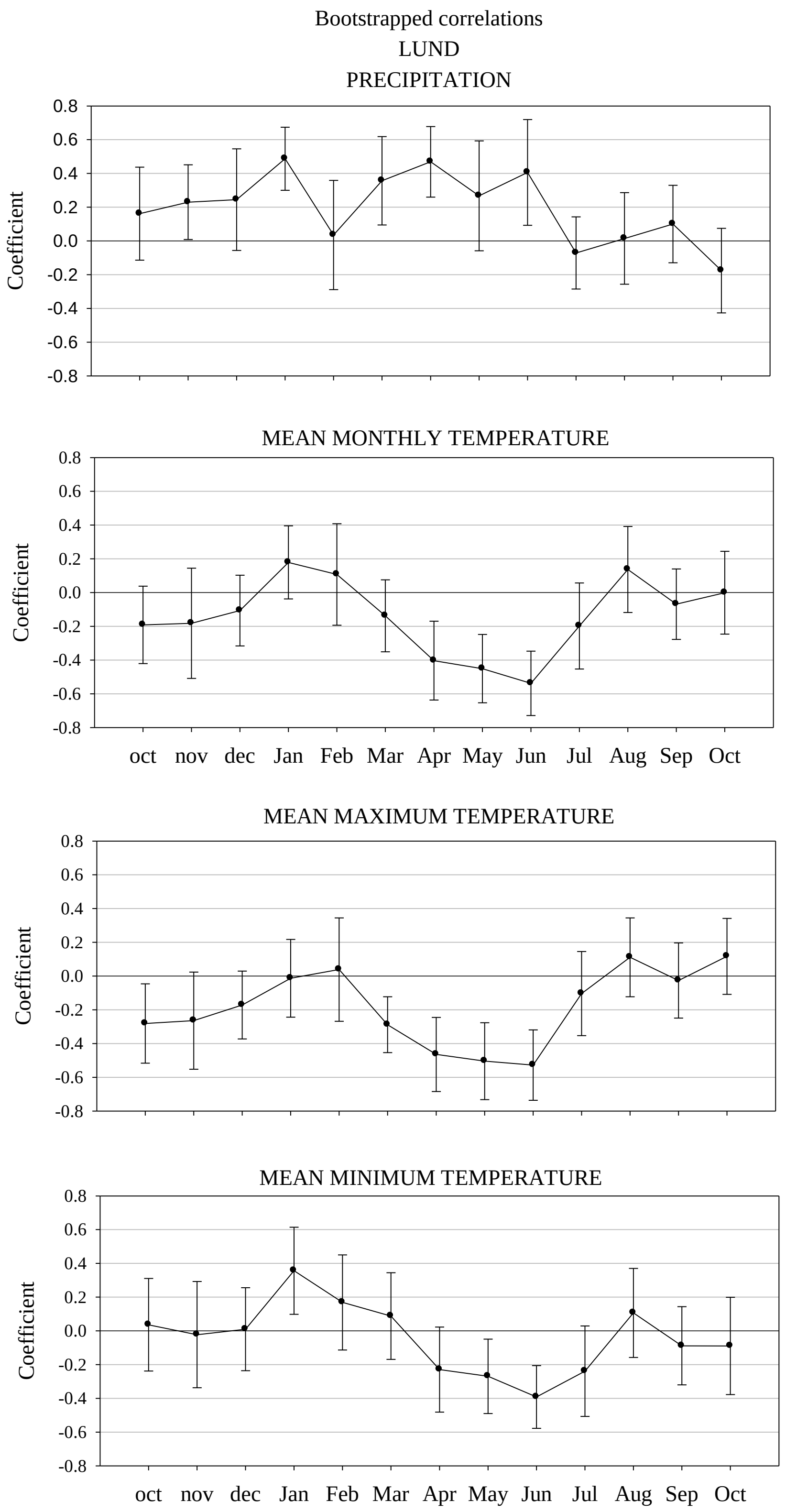


Figure 4.5 Bootstrapped monthly correlation results - Ely. Coefficients are shown with their 95% confidence interval ranges. The dashed line shows coefficient results from non-bootstrapped correlation analysis. Months from the previous year are not capitalized.



Bootstrapped correlations
LUND
PRECIPITATION

MEAN MONTHLY TEMPERATURE

MEAN MAXIMUM TEMPERATURE

MEAN MINIMUM TEMPERATURE

Figure 4.6 Bootstrapped monthly correlation results - Lund, Great Basin National Park, and Pioche. Coefficients are shown with their 95% confidence interval ranges. Months from the previous year are not capitalized.

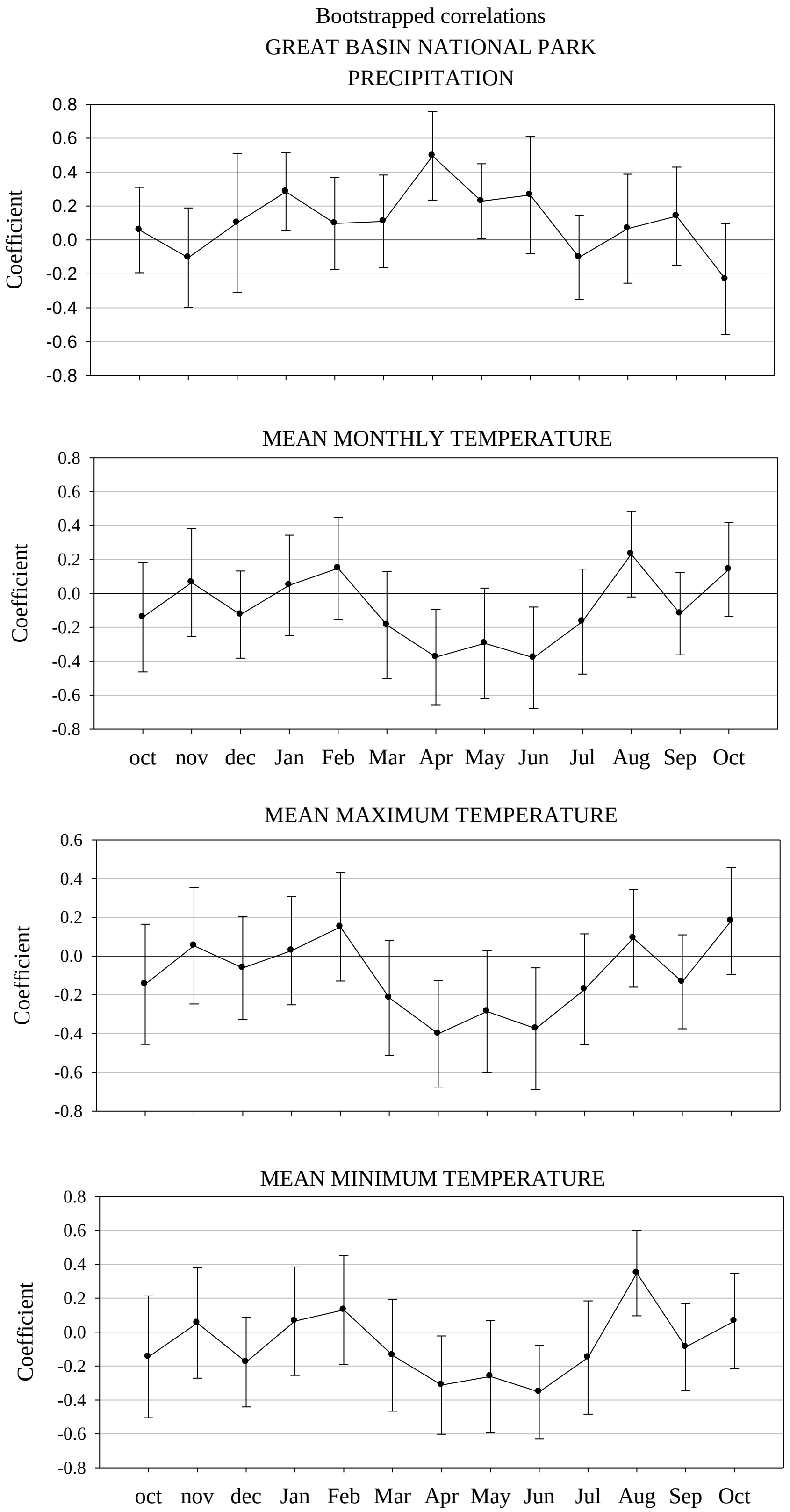
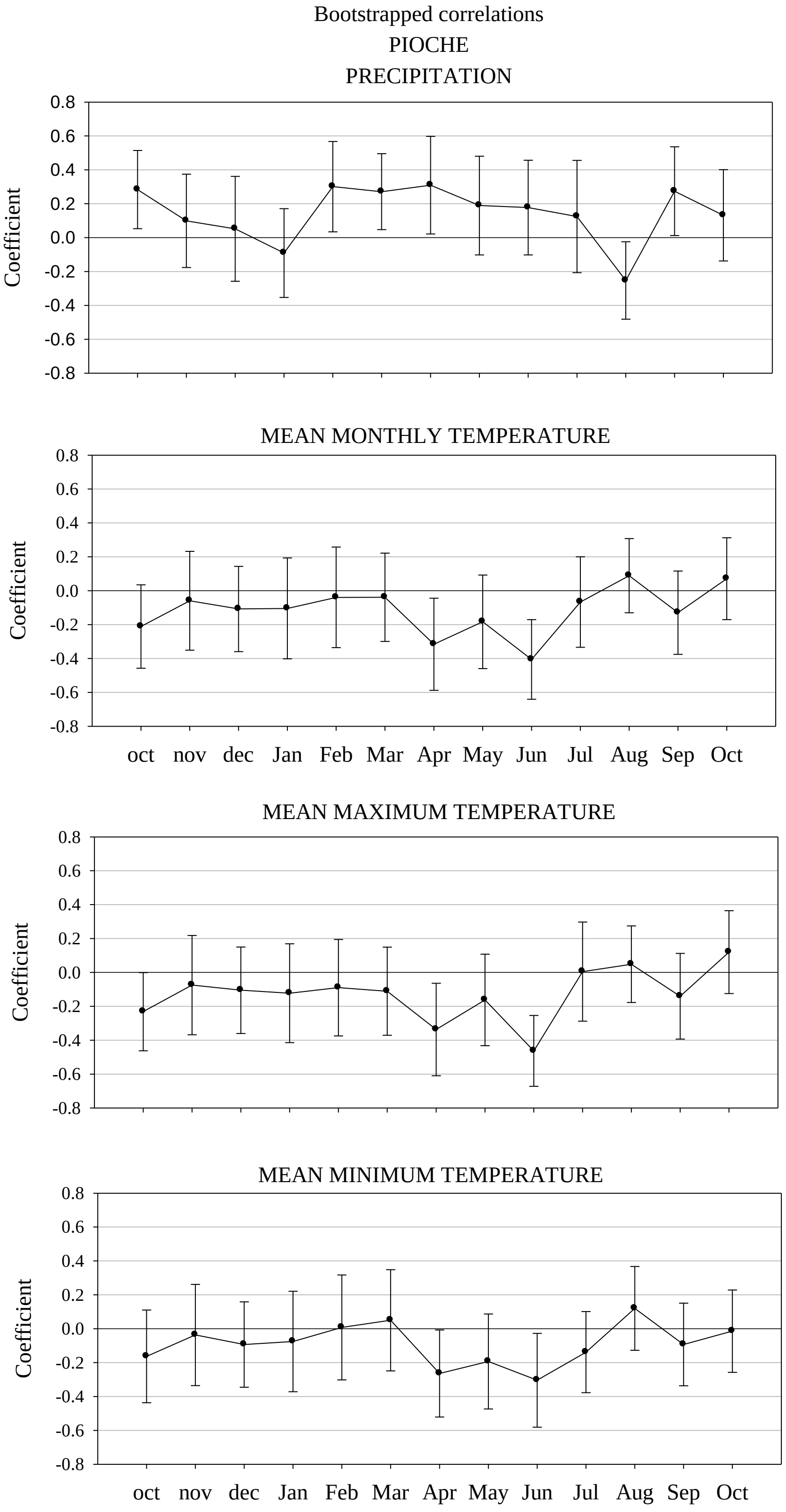


Figure 4.6 continued



Bootstrapped correlations
PIOCHE
PRECIPITATION

MEAN MONTHLY TEMPERATURE

MEAN MAXIMUM TEMPERATURE

MEAN MINIMUM TEMPERATURE

Figure 4.6 continued

Multiple regression analysis using both Shoshone Ranch maximum growing season temperature and annual growth year precipitation as independent variables produced the best regression relationship (adj. $r^2 = 0.72$, $p < 0.001$; Figure 4.7, left). The next best result came from a multiple regression between ring widths and Lund maximum growing season temperature and annual growth year precipitation (adj. $r^2 = 0.52$, $p < 0.001$; Figure 4.7, right). Results of all multiple regressions analyses are summarized in Table 4.6. Combinations of other precipitation and temperature data, including monthly measurements, various biologically-relevant time windows, and measurements from the other monitoring stations, did not produce better r-squared values compared to those summarized in Figure 4.7.

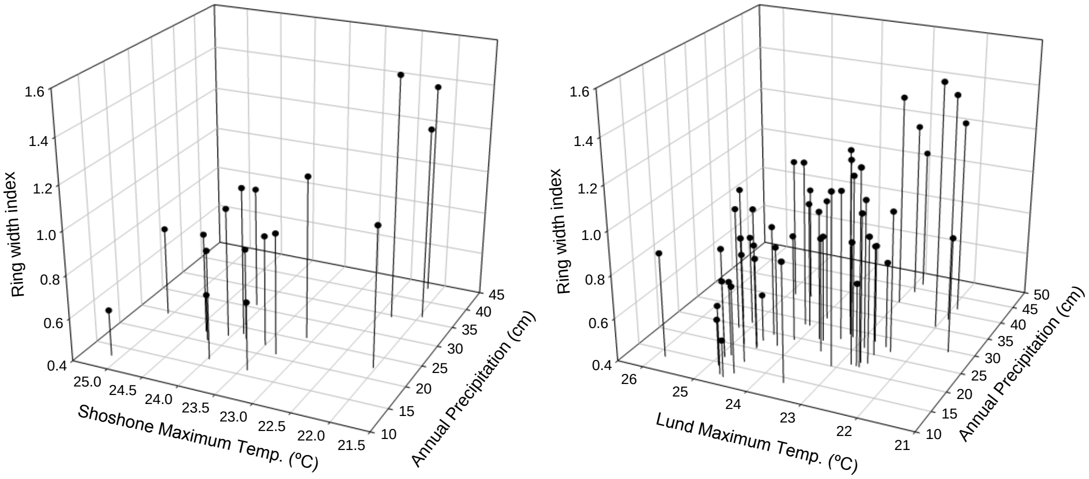


Figure 4.7 Sagebrush chronology versus Shoshone Ranch (left) and Lund (right) maximum temperature and annual precipitation. Plots indicate a clear negative relationship with increasingly arid growth conditions (low P, high T). Actual regression results are summarized in Table 6.

Sagebrush Rings and NDVI

Mean growing season NDVI demonstrated the best predictive relationship with Spring Valley annual ring growth ($r^2 = 0.48$, $p < 0.001$) during the common interval of 1987-2010. Figure 8 highlights how well NDVI tracks the changes in interannual growth ring width, but it also emphasizes the impact of pervasive cloud cover during rainy years, specifically the years of 1995 and 1998. Only two cloud-free Landsat images were available for 1995, and both of these images occurred in the last two months of the growing season (8/18 and 9/19). Four images were available throughout the 1998 growing season, but these images contained some degree of cloud cover either throughout the valley or around key calibration points. These problems resulted in mean NDVI values that appear much lower than expected when compared to similar peaks in the ring and NDVI series. However, retention of these values in the regressions always led an improved regression coefficient compared to analyses where these years were omitted, so those values were kept in the final regression (r-squared coefficient of 0.48 versus 0.45). Overall, NDVI values were very low thus to highlight the subtle differences in the NDVI, the y-axes in Figures 4.7 and 4.8 were set over a narrow range.

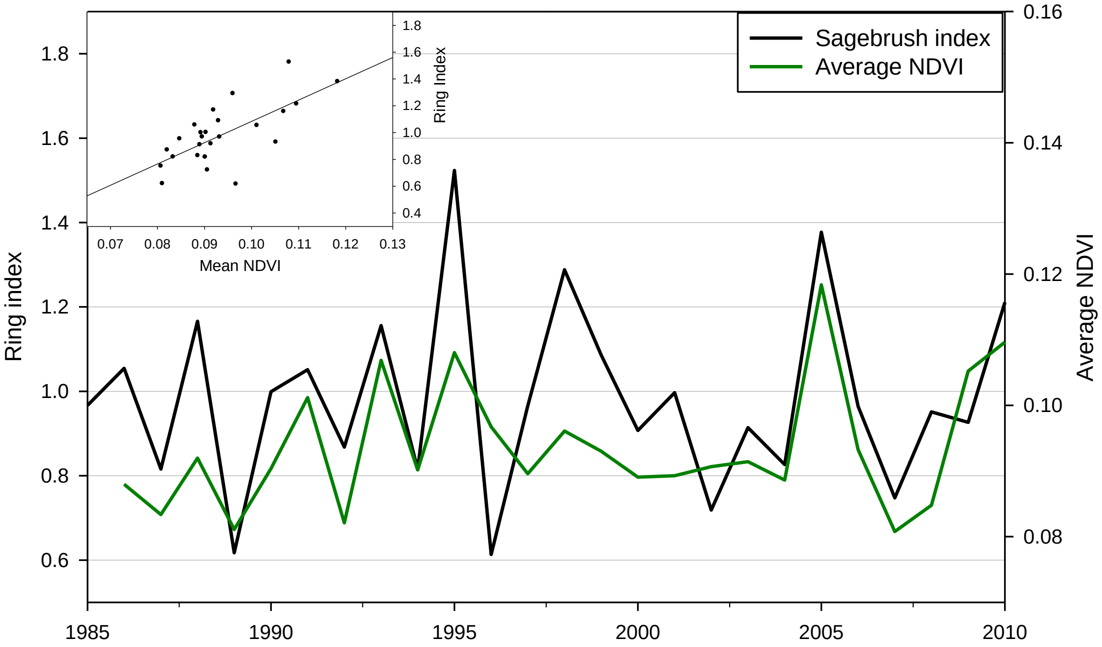


Figure 4.8 Comparison of the sagebrush chronology (black line) and the mean growing season NDVI of Spring Valley (green line) over the 1986-2010 common interval. Note the disproportionately low NDVI values occurring at 1995 and 1998 likely resulting from pervasive cloud cover. (Inset) Linear regression of these data sets showing a moderately good relationship between NDVI and sagebrush ring widths ($y = 15.9x - 0.05$; $r^2 = 0.48$, $p > 0.001$).

Regressions between both site-specific ring indices and NDVI measurements varied greatly among sites (Table 4.5). Site percent cover was shown to have a small, but significant ($p = 0.05$), impact on the strength of the individual regressions (Figure 4.9), where approximately 11% of the variation in ring width at all sites could be accounted for based on differences in vegetative cover.

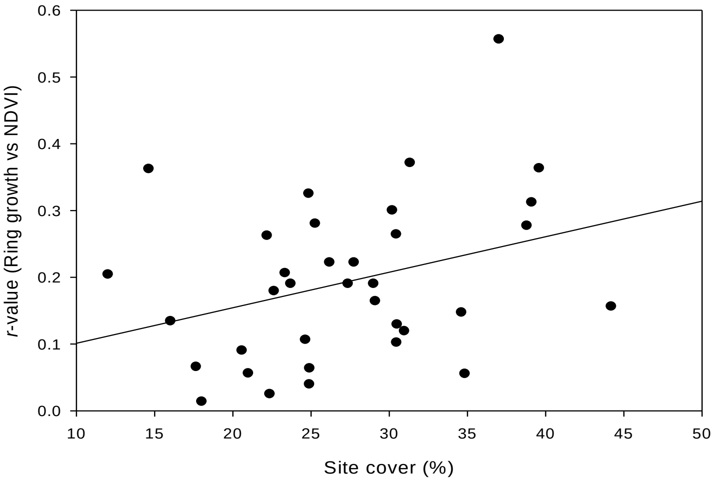


Figure 4.9 Regression plot of the ring-NDVI correlation coefficients versus site percent cover. The r-value on the y-axis was obtained from regression between individual site-specific ring chronologies and pixel-based NDVI values. (Fitted line: $y = 0.05 + 0.005x$; $r^2 = 0.11$, $p = 0.05$)

Mean bi-monthly NDVI values (1987-2010) revealed a distinct phenological pattern (Figure 4.10, top) similar to that found for sagebrush in Spring Valley (Baghzouz *et al.* 2010). NDVI rose sharply during May, coinciding with more favorable growing conditions, and peaked to a maximum growing season value in early June. A subtle decline in subsequent months (late June-August) was followed by a late-season growth peak in early September that doesn’t appear to be related to monthly precipitation or temperature. Regression between the ring index and bi-monthly NDVI (Figure 4.10, bottom) produced significant ($p < 0.05$) results between ring width and late May ($r^2 = 0.78$), early July ($r^2 = 0.68$), and early September NDVI values ($r^2 = 0.74$).

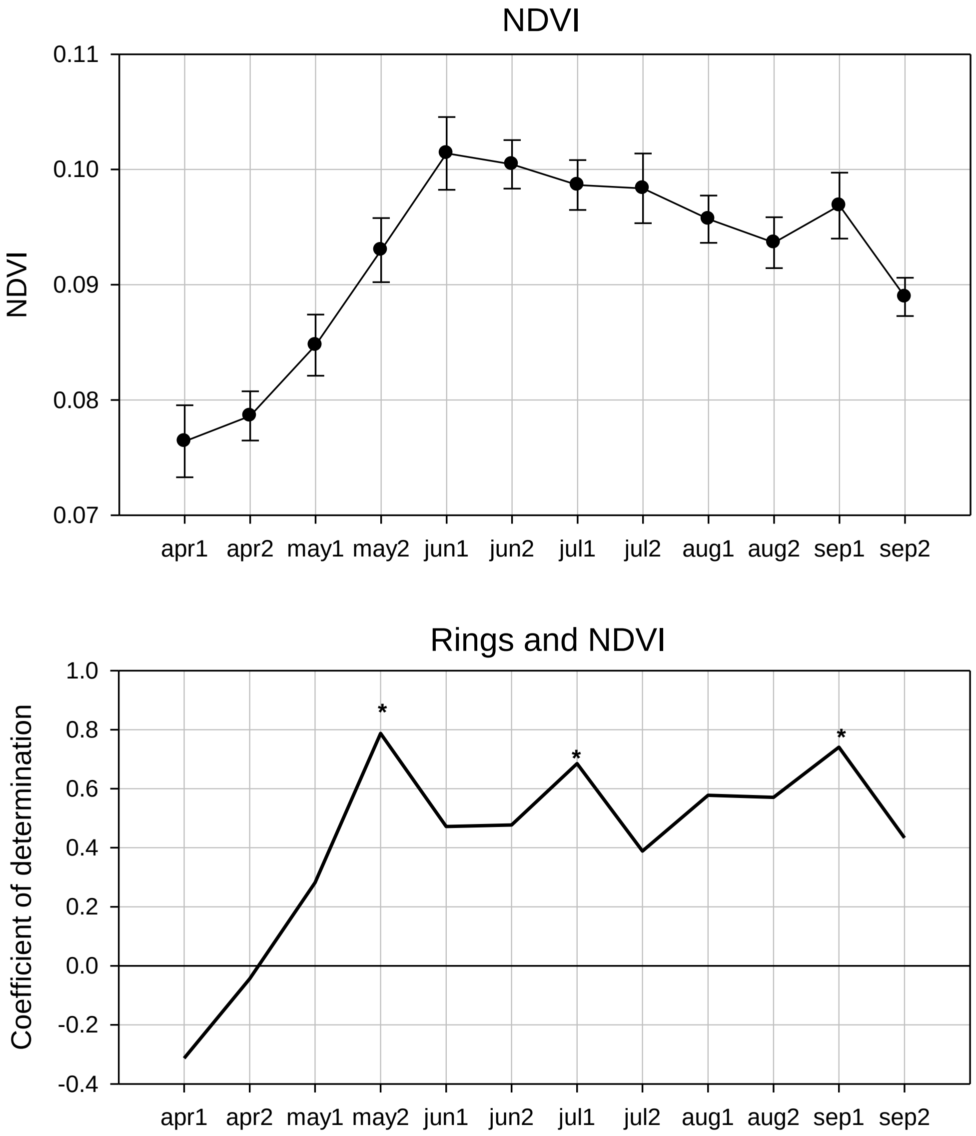


Figure 4.10 (Top) Bi-monthly NDVI over the April-September portion of the growing seasons of 1986-2010 and (Bottom) regression results between the sagebrush chronology and bi-monthly NDVI. The top graph highlights the highly productive month of May and peak canopy conditions of early June. Error bars denote the 95% confidence interval. (* $p < 0.05$).

CHAPTER 5

DISCUSSION

Climate change in Nevada is projected to be associated with increasing average temperatures (1.7 to 3.3 °C, EPA 1998) and decreasing water availability (Barnett *et al*. 2005, Seager *et al*. 2007) providing the impetus to understand more clearly the relationship between plant growth response and year-to-year climate variability. Therefore, the objectives of this study were: (1) to demonstrate the usefulness of big sagebrush (*Artemisia tridentata*) as a climate indicator by producing a viable sagebrush annual growth ring chronology representative of Spring Valley sagebrush stands using traditional dendrochronological methods, (2) to assess potential variation in growth attributed to small and large scale spatial heterogeneity by comparing the ring chronologies within the valley and across the region, (3) to examine the growth response of big sagebrush in Spring Valley to short-term climate variation by identifying the effects of climatic controls on radial stem growth and wood development, and (4) to establish an empirical relationship between growth ring chronologies and satellite-derived vegetation index data.

Spring Valley big sagebrush ring widths performed very well as proxies of interannual climate variability over a 70-year interval as demonstrated by their similarity in performance to other more common ring width proxies, such as bristlecone pines. Indexed ring width values showed high inter-series agreeability (Hypothesis 1) among all sagebrush present across the valley despite the problems inherent in sagebrush, notably the highly eccentric stem shape and tendency to produce absent or “false” ring patterns

(Ferguson 1964). Because extensive ring records for sagebrush are generally lacking, or in the case of Nevada, nonexistent, comparisons to a regional network of tree ring chronologies were made. Correlations between sagebrush and the tree network ($r = 0.30$-0.61, $p \leq 0.05$) revealed that sagebrush growth largely reflects growth in other woody species present throughout the region (Hypothesis 2). This lends credibility to the use of sagebrush in similar climate studies, although its usefulness for long-term reconstructions is greatly diminished by the relatively short longevity of the wood.

Sagebrush earlywood and latewood widths were statistically indistinguishable from total width measurements after the data were standardized. Earlywood and latewood chronologies have been used to more fully describe wood growth in relation to seasonal climate controls as differential growth between the wood types has been attributed to differences in seasonal resource availability (Lebourgeois 2000, Gonzalez and Eckstein 2003, Campelo *et al*. 2006, Vieira *et al*. 2009). Hypothesis 4 was based on observations made early on in the stem collection process where it was noticed that some samples showed a recognizable early/latewood pattern in which earlywood widths were very clearly different from the majority of the ring that was largely composed of darker latewood growth. With no quantifiable differences in their standardized widths, it appears that earlywood and latewood widths in Spring Valley sagebrush aren’t influenced by differing conditions in seasonal climate, and their growth is continuous throughout the season.

Correlation analysis revealed significant positive associations between sagebrush ring growth and winter precipitation totals ($r = 0.48$-0.67, $p < 0.001$; Hypothesis 3), but the strongest association existed between ring widths and total annual growth year precipitation (r = 0.53-0.82, p < 0.001). This, along with correlations between ring growth and monthly precipitation totals, revealed the sizeable contribution of warm-season precipitation (r = 0.52-0.68, p < 0.001) that was presumed to have a much smaller effect on growth based on previous studies showing winter precipitation being a major driving force on Spring Valley shrub leaf xylem water potentials and basin-wide evapotranspiration totals (Devitt *et al.* 2010). Donovan and Ehleringer (1994) documented the use of summer precipitation in sagebrush shrubs in Utah using hydrogen isotope composition analysis and attributed the ability of sagebrush to take advantage of sporadic summer rainfall events to the plant's extensive shallow root network. Conversely, one of the first dendroclimatological studies using big sagebrush, carried out by Ferguson and Humphrey (1959), found the strongest growth correlation with winter precipitation totals (November-April), and the effect of summer precipitation (May-October) was only noticeable when precipitation was more than twice that of winter. A more comparable study was conducted in Colorado by Poore *et al.* (2009) where a ring chronology was produced using a small sample (n = 5) of mountain sagebrush (ssp. *vaseyana*) and compared to various climatic measurements. They found a similar relationship between ring growth in mountain sagebrush and mean annual (November-October) precipitation (r = 0.63, p < 0.001), but seasonal comparisons showed a stronger correlation with wintertime precipitation (r = 0.68, p < 0.001) and a much weaker correlation with summer precipitation (r = 0.17, p = 0.315) than what was documented in this study (r = 0.68, p < 0.001). Winter precipitation response in Spring Valley sagebrush was found to be largely influenced by January precipitation, and precipitation during this month is most likely an indicator of the late-winter snowmelt occurring in February that helps drive spring growth in the valley.

The role of temperature was not included in the original hypotheses as the role of temperature on creating high evaporative demand was overlooked at first. Among Spring Valley sagebrush, mean maximum growing season temperatures had a significant and strongly negative effect on ring growth ($r = -0.78$, $p < 0.001$) with the most critical temperature maximums occurring during the March-June monthly interval. In the study of mountain big sagebrush by Poore *et al.* (2009), a similar, albeit weaker relationship was found between sagebrush ring growth and mean monthly temperatures measured during the May-October interval ($r = -0.62$, $p < 0.01$). In a study by DePuit and Caldwell (1973) found higher temperatures occurring later in the growing season were more optimal for photosynthesis in sagebrush leaves, but the effects of warmer temperatures on water availability were much more restrictive on carbon gain due to increased water stress. For sagebrush within Spring Valley, high maximum temperatures showed highly suppressive effects on sagebrush growth. Devitt *et al.* (2010) documented a steady increase in environmental demand (measured as ET_{ref}) in a Spring Valley mixed-shrub community over the April-June growing season period that reached its peak in July. This pattern of demand, which was highly dependent on temperature, typically peaks when water availability in the vadose zone has significantly declined (Wagner, personal communication). This was reflected in temperature correlations where maximum temperatures during these months, except for May and July, were highly related to ring widths in sagebrush plants during a given year (April, $r = 0.36$; May, $r = 0.47$; June, $r = 0.41$; all $p < 0.05$). The absence of any significant relationship from July onward, for either monthly temperature or precipitation, is likely an indication that wood production ceased before the more stressful late summer months occurred.

The controlling effects of climate were not strictly confined to the summer months as ring growth showed a significant negative relationship ($r = 0.30$, $p < 0.05$) with October maximum temperatures occurring during the preceding year recorded near Shoshone and Ely. Such a relationship could help explain the slight autocorrelative effects seen in the standardized ring chronology (ar1 = 0.246). Autocorrelation refers to the influence of a previous year's growth on growth during a subsequent year (Fritts 1976, Speer 2010), and the presence of autocorrelation in ring chronologies is not uncommon. Within Spring Valley shrub communities, October represents the end of the majority of photosynthetic activity, as evidenced by daily ET monitoring and plant physiological measurements (Devitt e*t al*. 2010). Excess carbohydrates in big sagebrush begin to accumulate around September, with the large majority of storage occurring in twigs (Coyne and Cook 1970). Plant water status, influenced by late-season maximum temperatures, could subsequently affect the carbohydrate reserves in sagebrush that could, in turn, influence the productivity of spring growth in the following year. These results lend evidence to the effects of late-season water status on future sagebrush wood production in Spring Valley.

Multiple regression analysis using ring widths and climate variables suggested that biological growth-year precipitation and maximum growing season temperatures exerted the greatest control on Spring Valley sagebrush growth. The resulting model incorporating those two variables was able to account for 72% (Shoshone Ranch data) of the total variance in sagebrush ring widths. Overall, the relationship between sagebrush growth rings and climate records highlight the plant's reliance on water availability but also on the environmental demand that is largely driven by high summer maximum temperatures. Sagebrush is well-adapted to take advantage of sporadic summer precipitation that is typically associated with late-summer monsoonal weather patterns in the Southwest due to its extensive shallow root network (Sturges 1977), but precipitation during these sometimes heavy rain events appears to have no significant effects on sagebrush wood production in the hottest part of the year as this moisture is quickly lost to evaporation and/or is used for other plant processes, such as the flower and seed production that occurs in later summer and early fall (Taylor 1992).

Based on the evidence presented here, the impact of projected climate change has the potential to be highly suppressive to sagebrush growth in Spring Valley. Warmer annual temperatures could directly inhibit growth by creating even greater environmental demand during the warmest months, and by extending the length of the growing season, this period of high demand could become extended. Warmer temperature during the winter months would result in more snow falling as rain and a subsequent reduction in the snowpack related to early season growth (Barnett *et al*. 2005). The impact in shifting precipitation regimes is less clear as projections for future precipitation are more conflicted, but effects of precipitation on sagebrush growth will be largely related to its timing. For example, increases in moisture availability outside of the most relevant months of January through June could have lesser effects on plant production, whereas increases within that key growth period could potentially counter the negative effects of water stress resulting from warmer temperatures.

There were a few limitations with the NDVI dataset that likely prevented the occurrence of higher regression coefficients between the vegetation index data and ring chronologies. The original series of Landsat images obtained from the EROS data center extended back to 1975. Prior to 1986, pixel resolution was coarser (90x90m as opposed to the current 30x30m resolution), but the more negative impact came from the incompatibility of these older images with available image processing software. Exclusion of these images significantly reduced the amount of available NDVI data. The range of NDVI values across all sites was relatively low (between 0.076 and 0.101), a characteristic that was noted for Spring Valley satellite-based measurements (Baghzouz *et al*. 2010). Each single pixel's reflectance value represents an integration of all the surfaces present within the 900 m^2 area covered by the satellite's synoptic view. With such low green cover at each sagebrush site (mean percent cover = 27%), satellite-based NDVI values are greatly influenced by the reflectance values of bare soil (Baghzouz *et al*. 2010). Also, 14 sites were characterized as mixed shrub communities and contained varying amounts of other plant species, each possessing potentially different phenology from sagebrush that could influence the overall pixel signal.

Perhaps the largest limitation encountered in the data set was the lack of quality reflectance values from two seemingly critical years – 1995 and 1998. Both of these years were characterized as highly productive growth years as evidenced by their high ring index values and high precipitation totals, but data were lacking due to pervasive cloud cover present in the majority of Landsat scenes taken during these two years that obscured much of the Valley floor and/or covered or shadowed points on the image used for atmospheric calibration. Attempts to mitigate the impact of cloud cover and shadows within the available images were unsuccessful.

Despite these problems, mean growing season NDVI integrated over multiple sagebrush sites revealed a significant relationship with sagebrush ring widths ($r^2 = 0.48$, $p < 0.001$), and mean bi-weekly values of NDVI had statistically significant regressions with ring widths during late May ($r^2 = 0.62$, $p < 0.01$), early June ($r^2 = 0.47$, $p < 0.01$), and early September ($r^2 = 0.54$, $p < 0.05$). These results indicated that NDVI can capture annual sagebrush growth ring production in Spring Valley throughout the growing season reasonably well (Hypothesis 5) despite the inherently weak vegetation signal, and this relationship could be used to estimate sagebrush growth trends in response to climate variation in the future. The regressions from this study are comparable to other studies that examined a similar relationship between NDVI and tree rings. Lopatin *et al*. (2006) reported significant relationships ($r^2 = 0.44 - 0.59$, $p < 0.05$) between NDVI and tree ring records representing the various vegetation zones of the boreal forest in the Komi Republic, Russia, where increases in productivity associated with NDVI were attributed to specific climatic controls. A study of spruce tree ring indices and integrated grassland NDVI (May-July) in north China (Liang *et al*. 2005) revealed a significant correlation ($r = 0.76$, $p = 0.003$) that was greatly attributed to variation in precipitation during key growth months. Wang *et al*. (2004) found a considerable correlation between average growing season NDVI and rings of oak trees assessed over what was considered an intermediate scale. The issue of scale comes into play when considering spatially heterogeneous areas such as Spring Valley, where distinct changes in topography contribute to a wide variety of vegetation zones over relatively short distances. By using the available Landsat image data (30x30m resolution), we were able to specifically resolve sagebrush growth trends where larger scaled data sets (such as Advanced Very High Resolution Radiometer (AVHRR), a common data set utilized in the literature) would invariably integrate reflective signals from other vegetation zones whose phenology may or may not reflect that of sagebrush present within mixed-shrub communities.

The extent to which this approach is feasible was tested by attempting to resolve an NDVI-ring relationship at the level of individual sagebrush sites, but this approach produced inconsistent results. Regressions between single-pixel NDVI and site-specific sagebrush ring chronologies produced relationships that were largely insignificant or greatly below the level of the valley-wide measures (mean $r = 0.27$) (Hypothesis 5). Much of the inconsistency with these site-specific results can likely be attributed to the high variability in ring index values when chronologies are constructed using smaller sample numbers even though inter-series correlations of ring widths were high, indicating local growth uniformity among a plant and its immediate cohorts. Larger sample numbers within each site would have likely averaged out some of the localized noise within the site-specific ring indices, possibly resulting in larger regression coefficients with NDVI.

Analyses from this study should help in highlighting the possible impacts of a rapidly changing climate on Nevada big sagebrush while also providing a method to help assess shrub growth in remote areas where related information is currently lacking. Uneven spatial coverage of climate records is a problem in climate studies in Nevada, as operational and well-maintained meteorological stations are typically associated with agricultural or population centers that Nevada has relatively few of compared to other states. With the abundance of sagebrush present throughout much of the state, growth ring studies like this one could be used to fill information gaps in climate records while remote sensing methods such as NDVI could be used to help assess ongoing vegetative changes that may occur. Results showed a clear negative impact of warmer temperatures and decreased precipitation on sagebrush growth. Changes to growth resulting from future climate change have great relevance to sagebrush steppe productivity, biodiversity, and valley hydrology. If the net impact of future climate change on Spring Valley sagebrush is negative, decreased growth could lead to a reduction in sagebrush cover, fragmentation of existing stands, and replacement of big sagebrush with more drought-tolerant or invasive species, in turn resulting in decreased habitat for sagebrush-dependent species. The identification of specific climatic controls on sagebrush growth provided here could lead to more informed range management practices and could be used to further enhance modeled effects of climate change on sagebrush steppe ecosystems.

APPENDIX A: TABLES

Table 1 Correlation matrix of all collected sagebrush sampling site variables and individual sagebrush plant and stem characteristics. Bolded values: $p \leq 0.05$.

	Mass	Height	Canopy volume	LAI	Stem area	Mean ring width	Sand	Cover	$EC_{surface}$	$EC_{profile}$
Ring Count	-0.272	-0.305	-0.229	0.180	0.167	**-0.426**	0.299	0.049	-0.066	-0.182
Mass		**0.681**	**0.797**	-0.047	-0.020	0.168	0.052	-0.204	0.304	**0.550**
Height			**0.775**	-0.135	0.010	**0.449**	-0.149	**-0.361**	0.136	0.305
Canopy volume				0.066	0.043	**0.324**	-0.157	**-0.364**	0.092	0.249
LAI					-0.302	**-0.361**	-0.073	0.168	-0.136	0.017
Stem area						0.083		-0.189	**-0.404**	**-0.332**
Mean ring width							-0.286	-0.182	0.129	0.078
Sand								-0.189	**-0.404**	-0.332
Cover									0.326	0.240
$EC_{surface}$										**0.759**

Ring count, mean number of rings measured within each site; Mass, total aboveground biomass measured in kg; Height, plant height measured in cm; Canopy volume, estimated elipsoidal volume (height * $width_1$ * $width_2$ * 4/3 * π, measured in m^3); LAI, leaf area index; Stem area, approximate cross-sectional area measured in cm^2; Mean ring width measured in mm; Sand, measured as percentage of particulate matter; Cover, estimated vegetative percent cover; $EC_{surface}$, electrical conductivity of 0-20 cm depth soil extracts measured in dS/m; $EC_{profile}$, mean soil profile (0-100 cm depth) electrical conductivity measured in dS/m.

Table 2 Statistics of climate station characteristics and monthly meteorological variables.

				Mean precipitation (SD) in cm			Temperature (SD) in °C		
Station name	Interval	Coordinates	Elev. (m)	Growth year[a]	Winter[b]	Growing season[c]	Mean	Mean max.	Mean min.
Shoshone	1989-2007	38°55'N, 114°24'W	1789	24.3 (7.6)	9.0 (4.8)	14.8 (4.8)	8.8 (0.8)	18.0 (1.0)	-0.4 (1.1)
Ely	1948-2010	39°18'N, 114°51'W	1908	23.4 (6.8)	8.7 (2.8)	14.7 (5.4)	7.0 (0.7)	16.2 (1.0)	-2.2 (0.8)
Lund	1958-2009	38°52'N, 115°01W	1690	25.3 (8.2)	9.8 (4.0)	15.6 (6.3)	9.0 (0.7)	18.3 (1.0)	0.4 (0.8)
Pioche	1939-2006	37°56'N, 114°27'W	1826	34.2 (11.0)	15.5 (7.3)	18.1 (7.1)	10.6 (0.8)	17.5 (1.2)	3.6 (0.8)
Great Basin National Park	1948-2010	39°00'N, 114°13'W	2088	33.5 (8.1)	13.5 (5.2)	20.0 (6.5)	9.0 (0.8)	16.0 (0.9)	2.0 (1.0)

[a] October-September, [b] October-February, [c] March-September

Table 3 Sagebrush ring width chronology statistics

	Record length	EPS interval	n_{stems}	n_{radii}	Mean ring width (SD)	Mean series length (SD)	r	MS	ar1	RMSE
Total width	1929-2011	1942-2010	103	247	1.03 (0.29)	39.5 (13.1)	0.613	0.37	0.246	--
Earlywood	1929-2011	1956-2010	71	147	0.32 (0.09)	37.6 (12.1)	0.405	0.392	0.326	0.09
Latewood	1930-2011	1942-2010	90	216	0.74 (0.25)	40.6 (13.2)	0.495	0.454	0.227	0.05

EPS, Expressed Population Signal,; n_{stems}, number of stems represented in the chronology; n_{radii}, total number of measured radii represented in the chronology; MS, mean sensitivity; ar1, first-order autocorrelation, r, mean series intercorrelation coefficient; RMSE, root mean square residual error between respective chronologies and total width chronology

Table 4 Tree network information and associated correlation statistics. Data collected from the NCDC NOAA International Tree-Ring database (http://www.ncdc.noaa.gov/paleo/treering.html)Pearson's *r* coeffcients were computed for overlapping time intervals between the sagebrush ring records (1942-2010) and Ely station precipitation (1949-2010) and temperature records (1939-2010). Bolded values: $p \leq 0.05$.

Code	Chronology Locations	Author	Species	Full interval	Latitude	Longitude	Elev. (m)	Distance (km)	Correlation (*r*) with sagebrush chron.
a	Mount Washington, NV	Graybill, D.A.	*Pinus longaeva*	825-1983	38.9	-114.32	3415	19.22	**0.309**
b	Hill 10842 Recollection	Graybill, D.A.	*Pinus longaeva*	0-1984	38.93	-114.23	3050	23.37	**0.500**
c	Horse Canyon Ridge	Thompson, M.A.	*Pinus monophylla*	1567-1978	39.27	-114.12	2347	40.16	**0.505**
d	Duck Creek Range West	Stockton, C.W.	*Pinus monophylla*	1570-1976	39.33	-114.75	2286	41.44	**0.549**
e	Egan Range West	Thompson, M.A.	*Pinus monophylla*	1465-1976	39.38	-114.92	2134	54.69	**0.563**
f	Pony Express	Stockton, C.W.	*Pinus monophylla*	1400-1982	39.82	-114.62	2210	89.38	**0.460**
g	Charleston Peak H-17 Saddle	Ferguson, C.W.	*Pinus longaeva*	966-1964	39.28	-115.63	3048	104.21	**0.602**
h	Panaca Summit	Stockton, C.W.	*Pinus monophylla*	1556-1982	37.77	-114.18	2103	141.1	**0.608**
i	Pearl Peak	Graybill, D.A.	*Pinus longaeva*	320-1985	40.23	-115.53	3170	159.7	-0.009
j	Mount Jefferson	Graybill, D.A.	*Pinus longaeva*	1300-1980	38.78	-116.95	3300	215.9	0.139
k	Pequap Summit	Stockton, C.W.	*Pinus monophylla*	1330-1982	41.05	-114.58	2286	220.49	**0.275**
l	Mammoth Creek	Graybill, D.A.	*Pinus longaeva*	0-1989	37.65	-112.67	2590	222.64	**0.494**
m	Wild Horse Ridge	Graybill, D.A.	*Pinus longaeva*	286-1985	39.42	-111.07	2805	299.08	**0.295**
n	Spring Mountains Lower	Graybill, D.A.	*Pinus longaeva*	320-1984	36.32	-115.7	3000	318.53	**0.400**
o	Jarbridge Canyon	Holmes, R.L.	*Juniperus scopulorum*	1334-1984	41.9	-115.42	1852	326.14	0.087
p	Jackson Mountains	Fritts, H.C.	*Juniperus occidentalis*	1267-1984	41.3	-118.43	2097	348.09	**0.299**
--	Spring Valley sagebrush	Apodaca, L.	*Artemisia tridentata*	1942-2010	various	various	ca. 1800	--	--

Table 5 Site-specific sagebrush ring chronology information and correlation coefficients between pixel-based NDVI measurements and ring data. Bolded values: $p \leq 0.01$.

Site ID	n_{rings}	r	r_{NDVI}	Site ID	n_{rings}	r	r_{NDVI}
SV1	63	0.768	0.0134	SV27	42	0.791	**0.363**
SV5	34	0.561	**0.312**	SV28	34	0.807	0.134
SV10	64	0.72	0.0655	SV29	55	0.786	0.119
SV12	45	0.661	**0.556**	SV30	28	0.684	0.0558
SV13	57	0.704	0.147	SV31	39	0.56	**0.325**
SV14	68	0.747	**0.19**	SV32	41	0.41	0.19
SV15	40	0.792	**0.371**	SV33	49	0.763	0.129
SV16	41	0.704	**0.222**	SV34	40	0.741	0.106
SV17	60	0.697	0.0634	SV35	45	0.837	**0.204**
SV18	64	0.689	0.0247	SV36	69	0.572	**0.179**
SV19	82	0.742	0.0394	SV37	52	0.633	**0.3**
SV20	69	0.775	0.102	SV38	46	0.641	0.09
SV21	36	0.801	**0.362**	SV39	47	0.693	**0.156**
SV22	41	0.789	**0.164**	SV40	63	0.398	**0.19**
SV23	25	0.44	**0.206**	SV41	55	0.742	**0.28**
SV24	56	0.51	0.0551	SV42	60	0.744	**0.277**
SV25	51	0.854	**0.264**	SV43	56	0.732	**0.222**
SV26	43	0.854	**0.262**				

n_{rings}, length of ring record in years; r, site-specific interseries correlation; r_{NDVI}, Pearson's coefficient between single pixel-based NDVI values and site-specific ring chronologies

Table 6 Multiple regression models between *Artemisia tridentata* ring chronology and two climatic variables, growth year precipitation and mean maximum growing season temperatures.

	$Y = b + m_1(x_1) + m_2(x_2)$					
Station	b	m_1	m_2	p	r^2	adj. r^2
Shoshone	3.801	0.017	-0.082	<0.001	0.75	0.72
Ely	1.277	0.017	-0.032	<0.001	0.48	0.46
Lund	2.121	0.012	-0.061	<0.001	0.50	0.52
Pioche	1.777	0.009	-0.049	<0.001	0.55	0.48
GBNP	1.932	0.009	-0.059	<0.001	0.35	0.32

m_1 = growth year precipitation (October-September) in cm.

m_2 = mean monthly max. growing season (March-September) temperature (°C)

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